CANADIAN THESES ON MICROFICHE

I.S.B.N.

THESES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL-339 (r. 82/08)

Canada

116

0-315-16025-X

National Library of Canada
Canadian Theses Division
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Division des thèses canadiennes

63934

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

• Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

John Stuart Richardson

Date of Birth — Date de naissance	Country of Birth — Lieu de naissance
6 April 1956	Canada

Permanent Address — Résidence fixe

Institute of Animal Resource Ecology
University of British Columbia
Vancouver, B.C.
V6T 1W5

Title of Thesis — Titre de la thèse

The effects of seston on the life history, growth, and distribution of Neureclipsis bimaculata (Trichoptera: Polycentropodidae) in a boreal river.

University — Université

Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M. Sc.

Year this degree conferred — Année d'obtention de ce grade	Name of Supervisor — Nom du directeur de thèse
1983	Dr. Hugh F. Clifford

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date	Signature
25 November 1982	John S. Richardson

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

The effect of seston on the life history, growth, and distribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a boreal river.

by

John S. Richardson

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Spring 1983

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR John S. Richardson

TITLE OF THESIS The effect of seston on the life history, growth, and distribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a boreal river.

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED Spring 1983

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) John S. Richardson

PERMANENT ADDRESS:

Institute of Animal Resource Ecology
Univ. of British Columbia
Vancouver, B.C. V6T 1W5

DATED 25 November 1982

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The effect of seston on the life history, growth, and distribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a boreal river. submitted by John S. Richardson in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

Date...16..November...1982...

ABSTRACT

A population of *Neureclipsis bimaculata* in a lake outlet stream was studied from November 1980 to September 1982. The life cycle was bivoltine during both years of the study. The summer generation was completed in only six to seven weeks, and the winter generation took the remainder of the year. Adult emergence took place from late May to early September, with two distinct peaks corresponding to the two generations. In both years the density of the summer generation exceeded that of the winter generation by at least an order of magnitude.

The amount and type of aquatic macrophytes were important in determining the larval distribution in this *N. bimaculata* population. Current velocity may also have been important in determining spatial distribution.

Maintenance of capture nets was seasonal, from May to September or early October. The timing of net building appeared to be related to temperature. High current velocities also seemed to affect net building; and in 1982, high velocities delayed net building by nearly a month from the date in 1981.

In a series of experiments *N. bimaculata* larvae were fed concentrated seston from either the lake outlet or a site 17 km downstream of the lake. The results showed that growth rates were significantly higher when larvae were fed seston derived from the lake outlet. At the time these experiments were performed, the amount ($mg \cdot l^{-1}$) of the

organic fraction of the seston was similar at both sites. However, inorganic particulate concentrations were much higher at the downstream site. These results suggest that larvae live at lake outlets because food quality is higher there than at downstream reaches.

A series of behavioural experiments examined the response of *N. bimaculata* larvae to placement of prey items in their capture nets. Many of the animals inserted into the net were able to escape from the net by swimming or crawling. Of the organisms trapped in the net, there was no difference in the form of the larval response. The main difference between prey types was the success with which *N. bimaculata* larvae were able to capture them. These results suggested that, although the larvae would feed on a variety of prey types, the net was most efficient at capturing *Daphnia*, of the prey items tested. *Neureclipsis bimaculata* populations may occur at lake outflows because of the abundant supply of small prey, i.e. zooplankton caught in the water leaving the lake.

ACKNOWLEDGEMENTS

I thank Dr. Hugh F. Clifford for acting as my supervisor during the course of this work. Drs. John Aho, and J.J.H. Ciborowski, and Mr. Vytenis Gotceitas critically reviewed the manuscript, greatly improving the text, for which I am indebted. Thanks are due to Dr. W. Mackay for making all the facilities of the Lac Ste. Anne Fisheries Research Station available.

I would like to thank all those who accompanied me in the field at various times and particularly Teresa Lovell, Roberta Miller and Elizabeth Thomson for their capable assistance in the laboratory and field. I'm also grateful for the assistance of Mrs. Getrude Hutchinson.

I thank my labmates, particularly R.L. Baker, J.J.H. Ciborowski, V. Gotceitas and D.A. Soluk, members of the freshwater benthic discussion group and other members of the Department of Zoology for valuable discussions. Drs. C. Cushing, D.M. Rosenberg, H. Tachet and J.B. Wallace were very courteous and generous in sharing unpublished data and observations about *Neureclipsis* with me. Brian Husband (Department of Botany) kindly identified the aquatic macrophytes. Dr. John Aho identified the gregarine.

I gratefully acknowledge the financial support of the Boreal Institute for Northern Studies, a NSERC postgraduate scholarship and a NSERC operating grant to Dr. Hugh F. Clifford.

Table of Contents

Chapter

Page

THESIS INTRODUCTION 1

CHAPTER ONE

Life cycle and ecology of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a lake outflow stream, Alberta, Canada. 5

Introduction 5

Materials and Methods 6

Study Site 6

Sampling 9

Results 13

Life Cycle 13

Microdistribution 21

Population Dynamics 23

Discussion 27

Life History 27

Microdistribution 33

Population Dynamics 35

General Discussion 37

CHAPTER TWO

Seston dynamics and their influence on the growth and distribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) larvae in a boreal river, Alberta. 39

Introduction 39

Study Area 41

Materials and Methods 41

Results 45

Seston Dynamics 45

Growth Rates 51

Discussion 54

Seston changes and growth of *N. bimaculata* 54

Effects of seston quality 59

Other patterns of population distribution .60

Effects of seston on life history 61

Other factors affecting distribution 63

CHAPTER THREE
The feeding behaviour of *Neureclipsis bimaculata* larvae (Trichoptera: Polycentropodidae). 65

Introduction 65

Materials and Methods 66

Results and Discussion 70

Behaviour 70

Feeding Experiments 71

CHAPTER FOUR
The determination of a sex-related size dimorphism in larvae of *Neureclipsis bimaculata*. 79

Introduction 79

Methods and Materials 80

Results and Discussion 80

THESIS DISCUSSION 87

What determines the distribution of *Neureclipsis bimaculata* populations ? 87

Conclusions and Future Research 90

Literature Cited 91

Appendix 1: Total numbers of *N. bimaculata*

larvae, prepupae, and pupae per sample. Only completely sorted samples included. Samples with no individuals not listed. 98

Appendix 2: Numbers of samples of fourth and fifth instar larvae used for population estimates. Only samples collected in the Lee sampler included. 99

Appendix 3: Response times of *N. bimaculata* larvae to different prey items in the net (seconds). Only includes prey items to which larvae responded. 100

Appendix 4: Preliminary list of the invertebrate taxa found in the Sturgeon River at Lac Ste. Anne, Alberta. 101

List of Tables

Table — Page

1 Geometric mean dry weights (mg) of each instar of *Neureclipsis bimaculata* larvae. 12

2 Head widths of each instar of *Neureclipsis bimaculata* larvae in mm. 14

3 Table of significant product moment correlations between densities of *Neureclipsis bimaculata* and microhabitat variables. 24

4 Production estimate calculations according to the instantaneous growth method. 28

5 Percent increase in individual wet weight of *Neureclipsis bimaculata* larvae after 8 days of feeding under experimental conditions. Means ±standard error and N. 52

6 Summary of objects inserted into the net of *N. bimaculata*. 68

7 Number of responses to prey landing in different parts of the capture net. 73

List of Figures

Figure — Page

1 A. Map of the Sturgeon River at the outlet of Lac Ste. Anne, Alberta. The four stratified sampling areas are marked A, B, C, D. B. Inset map of Alberta showing location of the study site. 8

2 Water temperatures of the Sturgeon River during the sampling period. Mean weekly temperatures and their ranges are shown for most of the year; black dots indicate single temperature readings. 15

3 Estimates of discharge ($m^3 \cdot s^{-1}$) in the Sturgeon River at the outlet of Lac Ste. Anne during the summers of 1981 and 1982. 16

4 Life cycle of *Neureclipsis bimaculata* in the Sturgeon River from November 1980 to June 1982. A. Histograms represent relative percentage of total individuals in each stage. Numbers over the histograms are the sample sizes. P includes prepupae and pupae. B. Schematic life cycle based on mean stage at each sampling date. Dotted line represents adult flight period. 17

5 Emergence phenology of *Neureclipsis bimaculata* adults captured in floating traps on the Sturgeon River. Males shown by stippling, females by crosshatching. Note logarithmic scale for numbers/ trap/ day. 19

6 Seasonal phenology of *Chara* sp., *Potamogeton richardsonii* and total plants based on percentage cover in samples. 22

7 Population estimates of *Neureclipsis bimaculata* for larval instars IV and V, and total individuals (including all larval instars, PP and P) from benthic samples. Geometric means ±95% confidence intervals. Note logarithmic scale. 26

8 Map of the Sturgeon River in the study area. The six sampling stations are identified by numbers except for the Lake and Onoway sites. Inset map of Alberta shows location of study area. 42

Figure Page

9 Seasonal seston dynamics at the outlet of Lac Ste. Anne (closed circles, solid line) and Onoway (open squares, dashed line). Upper graph is the organic component (OPM), lower graph is the inorganic component (IPM). Note difference of scale between graphs. 46

10 Seston dynamics for a 10-day period in August 1982 showing short-term fluctuations. In Figure 9 these data are combined in one point per curve. Symbols as in Figure 9. 47

11 Percentage composition of particulate matter in transport, Sturgeon River. Mid-day samples collected 17 August 1982 (Lake), and 13 August 1982 (Onoway). 49

12 Downstream changes in particulates in the Sturgeon River between Lac Ste. Anne and Matchayaw Lake (denoted by arrow). Six points correspond to six sampling stations shown in Figure 8. Means ±95% confidence intervals. 50

13 Results of laboratory experiment 2 showing differences in the instantaneous growth rate of larvae fed one of two types of seston. Means ±95% confidence intervals. 53

14 Results of the field experiment showing the instantaneous growth rates of larvae. Means ±95% confidence limits. 55

15 The capture net of a fifth instar *Neureclipsis bimaculata* larvae showing component parts. Arrow indicates direction of flow. 69

16 Frequency of response distances to different food types. 75

17 Head of *N. bimaculata* larva showing the dimensions measured. HW=head width, FCL=frontoclypeal apotome length, FCW=frontoclypeal apotome width. 81

18 Head width frequency histograms of fourth and fifth instar larvae and prepupae of *N. bimaculata*. 82

Figure Page

19 Plot of frontoclypeal apotome size from pupae of *Neureclipsis bimaculata*: males are closed squares, females are open squares. 84

20 Plot of the relationships between head width and frontoclypeal apotome dimensions in a series of fifth instar larvae. 85

THESIS INTRODUCTION

Studies of distribution patterns of organisms can focus on a variety of different spatial scales. Zoogeographic (species level), population (regional), intrapopulation (microdistribution) patterns, etc. can all be examined. Ecological studies of aquatic invertebrates have most often focussed on microdistribution or zoogeographic patterns.

Often a major difficulty in testing hypotheses about population distributions is adequately defining a population. However, some freshwater invertebrates have restricted ecological requirements making populations easy to define. One such organism is the filter feeding caddisfly *Neureclipsis bimaculata* (L.) (Trichoptera: Polycentropodidae). This animal is restricted to lake outflow stream reaches and rarely occurs more than about 1.5 km from a lake source (Statzner 1978, Edington and Hildrew 1981). This makes it possible to generate several hypotheses as to why this species is primarily found at lake outlets.

First, one needs to consider what changes in the physical and biotic environment of rivers occur downstream from lakes. It has been shown that seston (defined as all particulate matter suspended in the water) in rivers changes as it moves away from lakes. At lake outlets there is a high concentration of planktonic organisms such as copepods, cladocerans and algae trapped in the water draining from the lakes (Chandler 1937, Maciolek and Tunzi 1967, Armitage and

Capper 1976). These organisms are lost to predation, killed by current, or other sources of mortality downstream, and seston becomes increasingly composed of refractory materials such as detritus and faeces (Maciolek and Tunzi 1967, Benke and Wallace 1980). With the large number of invertebrates of relatively uniform size distribution in the seston at lake outlets, a predator could specialize behaviourly, morphologically, or both, to exploit this type of prey.

Along with the organic material transported by streams are inorganic particulates, sometimes referred to as silt. To a filter feeding organism, inedible particles landing in the filtering apparatus can reduce feeding efficiency by clogging the filtering device or by being ingested reducing the rate of caloric intake. Since lakes act as silt traps, outlet streams will have lower amounts of suspended inorganic particulate material than downstream reaches (Armitage 1976).

Temperature regimes may be less variable at lake outlets than in rivers not associated with lakes. Winter water temperatures may be slightly higher in lake outlets than in downstream reaches because many lakes stratify, allowing some invertebrates to exploit these conditions to continue growth. Higher lake outlet temperatures also reduce chances of freezing.

Fluctuations in discharge rate could be of lower amplitude, although of longer duration, at lake outlets, since the immediate effect would be damped by the lake

(Armitage 1976). A filter feeding animal that maintains some form of filtering apparatus may be better able to adapt to slow changes in discharge than sudden spates. This could be by relocation to a more suitable microhabitat for invertebrates generally, or by altering the form of the net by filter feeding caddisflies. Related to this large-scale variation in discharge is short-term variation in current velocity, i.e. large-scale turbulence. Due to the geomorphological character of lake outlets, outflow stream reaches tend to be broad and shallow (Carlsson *et al.* 1977). For an animal that constructs a rather flimsy net, as in *N. bimaculata*, there may be limits to the amount of variation in current velocity a net can withstand. Since turbulence is partially related to depth (Smith 1975), outlet reaches should exhibit relatively less turbulence than deeper, narrower downstream reaches.

All of these characteristics of lake outflows may be important in determining the distribution of *Neureclipsis bimaculata* populations. Also, biotic influences such as competitive exclusion or predator evasion can determine distributions of some organisms.

First, I set out to describe the natural history of a population of *N. bimaculata* in the Sturgeon River at the outlet of Lac Ste. Anne, a relatively large but non-stratifying lake of central Alberta. I wished to consider the general hypothesis that the distribution of a population of *N. bimaculata* is determined by adaptation of

its larvae to the suite of characteristics of lake outflow stream reaches discussed above. To test this hypothesis, I formulated predictions, and experiments were designed to address these. The first set of experiments were designed to investigate the effect that downstream changes in seston had on the growth of *N. bimaculata* larvae. A second experiment dealt with potential specialization on certain prey types, by examining the response of *N. bimaculata* larvae to capture of different types of potential prey.

CHAPTER ONE

Life cycle and ecology of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a lake outflow stream, Alberta, Canada.

Introduction

Ecological study of freshwater invertebrates, particularly immature insects, has been severely hampered by taxonomic difficulties. The natural history of many species is poorly or not known. These problems have restricted our ability to generate broad hypotheses about the ecology of aquatic organisms. The need for basic life history data and ecological hypothesis generation has been addressed by Waters (1979).

Neureclipsis bimaculata (L.) (Polycentropodidae) is holarctic in distribution. In North America it is found throughout Canada and the northern United States (Nimmo in press). Larvae live in slow moving water associated with lake outflows or large rivers where they construct silk capture nets on any available substrate (Wesenberg-Lund 1911, Brickenstein 1955, Lepneva 1964, Edington and Hildrew 1981). These nets are used to filter seston, including copepods and cladocerans, from the water column. Larvae are considered predaceous based on gut contents (Popowa 1927, Hynes 1970, Wiggins 1977, Wallace *et al.* unpublished manuscript).

Most references to the life cycle of *N. bimaculata* have indicated a wide range of larval sizes throughout the year. A life cycle of 2 years has been inferred for north European populations (Wesenberg-Lund 1911, Alm 1926). Statzner (1979) concluded that *N. bimaculata* populations had a 1 to 2 year life cycle in northern Germany. The only known work on *N. bimaculata* in North America suggested a 1 year life cycle in northern Alberta, Canada (Robertson 1967). Populations can have long emergence periods, lasting 2-4 months during the summer over most of *N. bimaculata*'s range (Brickenstein 1955, Hickin 1967, Nimmo in press).

My work was undertaken to determine the life cycle and investigate the population dynamics of *Neureclipsis bimaculata* in the Sturgeon River, Alberta. In addition larval sampling was designed to answer questions about the microdistribution of *N. bimaculata* larvae. Questions included (1) what is the influence of current speed on the microdistribution, (2) what is the importance of substrate type on the distribution, and (3) are there instar-specific or seasonal patterns of microdistribution?

Materials and Methods

Study Site

The Sturgeon River is a slow moving stream of the boreal forest region in Alberta, Canada (53°42' N, 114°19' W). In the study area, a 1 km reach at the outflow

of Lac Ste. Anne, the Sturgeon River is a third-order stream with a drainage basin of approximately 700 km². Land use in the drainage basin is primarily for livestock grazing and for recreational purposes. Lac Ste. Anne has a surface area of 57 km² , average depth 4.8 m, and does not stratify. The mouth of the river was defined by a weir near the road (Figure 1).

The river descends 6.4 m in the first 6 km below Lac Ste. Anne. Average width was about 17 m, and in 1981 maximum depth was 80 cm in the study area; in 1982, heavy rains increased maximum depth to about 120 cm. Current velocities ranged from zero to about 42 $cm \cdot s^{-1}$. During 1981 most current speed measurements were between 3 and 10 $cm \cdot s^{-1}$. Velocities were higher in 1982, generally between 15 to 25 $cm \cdot s^{-1}$ in the centre of the stream. The substrate is soft, mostly sand and silt; cobbles, larger mineral particles and deadfalls cover very small areas. The first 500 m of the river downstream of the lake is bordered by few trees, streamside vegetation being mainly sedges on a wide floodplain. The area further downstream is bordered by dense stands of aspen (*Populus tremuloides* Michx.). During the study period most of the river margin was lined with *Typha latifolia* L. and patches of *Equisetum* sp. Predominant aquatic macrophytes were *Chara* sp., *Potamogeton richardsonii* (Benn.)Rydb., *Myriophyllum exalbescens* Fernald, *Potamogeton pectinatus* L. and *Lemna trisculca* L.

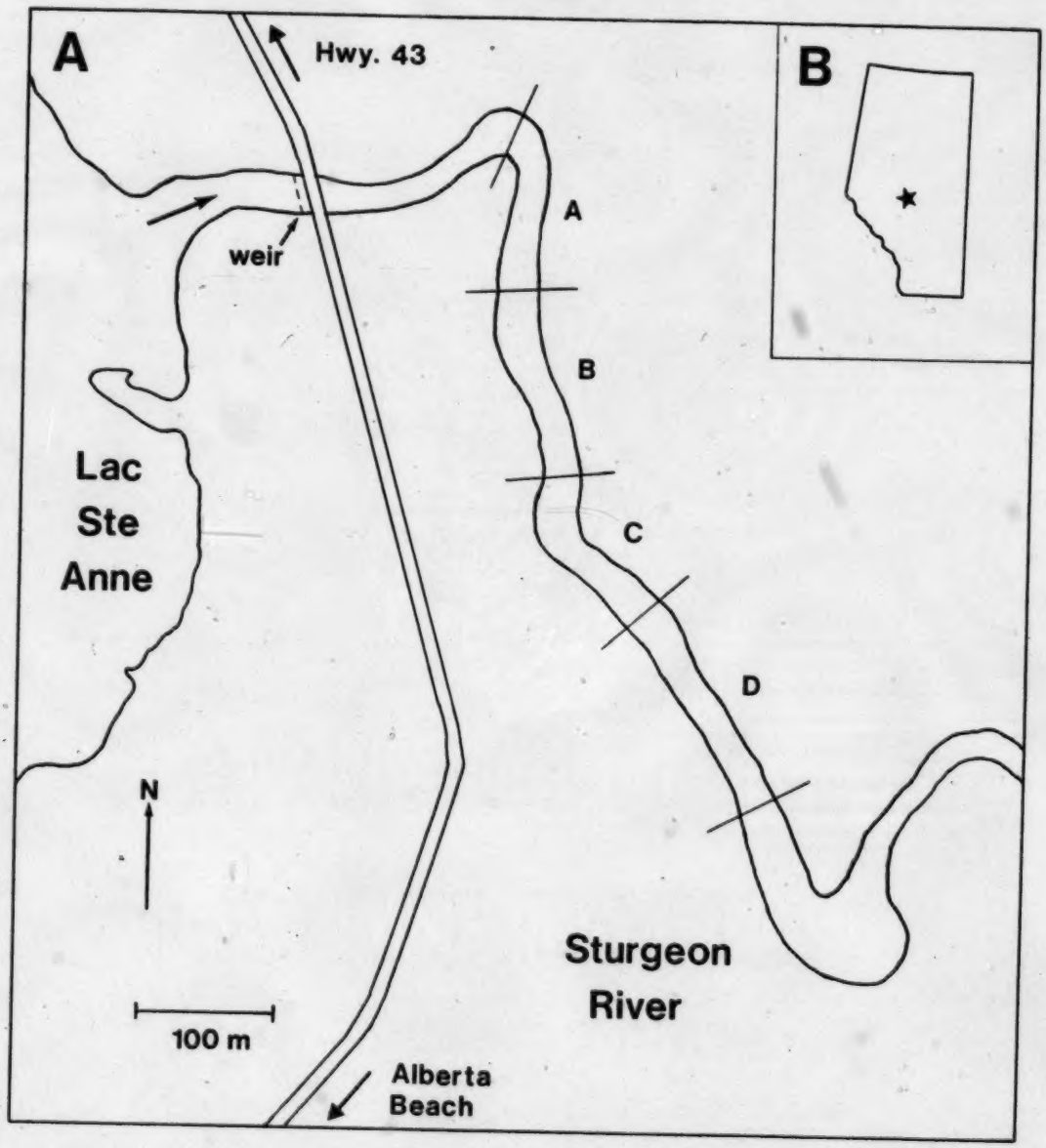

Figure 1. A. Map of the Sturgeon River at the outlet of Lac Ste. Anne, Alberta. The four stratified sampling areas are marked A, B, C, D. B. Inset map of Alberta showing location of the study site.

Sampling

Samples were collected from November 1980 to December 1981 using a "Lee" sampler (except January to April 1981). This is a box-type sampler (Merritt *et al*. 1978), 59 cm high, with a wire screen on the upstream side (mesh opening 1 mm) and a net on the downstream side (mesh size=150 μm). The bottom edge of this sampler penetrates the substratum, and encloses an area of 945 cm^2. From January to April 1981, samples were taken using a coring device (diameter=4.7 cm). High water levels in 1982 precluded use of the "Lee" sampler, and samples in 1982 were taken using a modified Ekman dredge (area=256 cm^2) attached to a pole.

From 19 May 1981 to 7 December 1981, samples were taken along transects according to a stratified sampling scheme. On each date, four to six samples were collected from 3 m intervals along a transect in each of four zones. New transects were sampled in each zone on each date to avoid sampling a previously disturbed area. On dates other than those between 19 May and 7 December 1981 samples were not collected along transects, but were still collected within the four zones. The substratum was sampled to a depth of about 5 cm, and all substratum1 including plants, was collected.

During 1981, I recorded position of the transect, distance from the shores, depth, current velocity (using an Ott current meter, model C2), plant composition and percent cover of plants for each sample. Percent cover was

estimated as the area covered by each plant type in a sample delimited by the "Lee" sampler. Samples were preserved in the field in Kahle's solution (2% acetic acid, 28%-95% EtOH, 11% formalin, 59% water) for later processing.

In summer, temperature data were collected using a Ryan continuous recording thermograph. During other seasons only spot water temperatures were recorded. Cumulative degree days were calculated using 0°C as the base.

Floating emergence traps (Merritt *et al.* 1978) were used from 4 August to 14 September 1981 and 27 May to 27 September 1982. They were emptied approximately twice a week in both years. A trap consisted of a floating wooden and styrofoam frame, enclosing an area of 0.25 m^2, with a fine-meshed tent-shaped net with a transverse "shelf" inside. An inverted funnel inside a glass collecting jar at the top of the trap retained emerging insects.

In the laboratory, samples were sieved into two size fractions: coarse (≥0.85 mm) and fine (<0.85 mm and ≥0.25 mm). Cursory examination of a few samples for larvae passing through the 0.25 mm sieve yielded no small larvae; hence I was confident that few animals passed through the 0.25 mm sieve. The fine fraction was elutriated to separate organic matter from the mineral portion. Samples were examined under a dissecting microscope at 6X power. During sorting, samples were subjectively scored on a 3-point scale for the amount of organic material they contained (1=very little organic matter, 3=highly organic).

Representative *Neureclipsis bimaculata* larvae and prepupae (as defined by Wiggins 1977) from all sampling dates were measured across the head using an eyepiece micrometer to the nearest 0.024 mm. All specimens were from the population at the outflow of Lac Ste. Anne. Larval instars were determined by the head width frequency method (Resh 1976). Larvae were separated into instars and counted. Larval instars are referred to throughout as L-I, L-II, etc., and prepupae and pupae are abbreviated to PP and P, respectively. During the entire sampling period only one individual of another polycentropodid, *Polycentropus remotus* Banks, was collected; therefore I assumed that even very small larvae were *N. bimaculata*.

For many samples only the coarse size fraction was sorted to yield individuals in the fourth instar or older. However, only completely sorted samples were included in the life cycle analysis and population estimates.

Microdistribution of *Neureclipsis* larvae was analyzed by product moment correlations and a multiple regression of larval density against a series of environmental variables. These procedures determined the variables most important in influencing larval distribution.

Representative larvae and pupae were dried at 50°C for 24 hours to determine dry weights (Table 1). These data were used in the calculations of production based on the instantaneous growth method (Waters 1977).

Table 1. Geometric mean dry weights (mg) of each instar of *Neureclipsis bimaculata* larvae.

Instar	Mean	95% Confidence Interval	N	Range
♀ V	4.09	3.340 - 4.980	30	1.358 - 9.490
♂ V	2.23	1.920 - 2.570	35	0.530 - 3.618
IV	0.54	0.490 - 0.600	112	0.139 - 1.748
III	0.127	0.110 - 0.140	49	0.042 - 0.280
II	0.033	0.029 - 0.036	21	0.020 - 0.047
I	0.005		25	

Results

Life Cycle

Temperature and discharge data for the study site are shown in figures 2 and 3. Temperatures were generally lower during 1982 than in 1981. Ice went off the lake in early April, 1981, and in the middle of May, 1982. In 1981 discharge was relatively normal for the site, whereas 1982 was a year of high discharge. Available data (Water Survey of Canada, Environment Canada) suggest discharge was at a 10-year high in 1982.

Five larval instars were identified for the *N. bimaculata* population (Table 2). There were no differences in the distribution of head sizes between generations or seasons. There were pronounced size differences between the sexes of instar L-V; this is evident as a bimodal distribution in the frequency of head widths (see chapter 4). The bimodal form of the frequency distribution of L-IV head widths was less pronounced.

The population appeared to be bivoltine at the study site with a winter and a summer generation. The winter generation is derived from eggs laid in August and September, overwinters as larvae and emerges from late May to early July. The summer generation begins as eggs oviposited by winter generation adults and is completed by late August or early September. Larvae overwinter in instars L-II to L-V, but mostly in instar L-III (Figure 4). In 1981, pupae and prepupae were first found on 19 May and

Table 2. Head widths of each instar of *Neureclipsis bimaculata* larvae in mm.

Instar	Mean	Standard Deviation	N	Range
♀ V	1.23	±0.101	198	1.128- 1.344
♂ V	1.04	±0.058	279	0.936- 1.128
IV	0.75	±0.153	806	0.600- 0.864
III	0.47	±0.033	195	0.408- 0.528
II	0.30	±0.009	120	0.264- 0.336
I	0.19		25	0.190

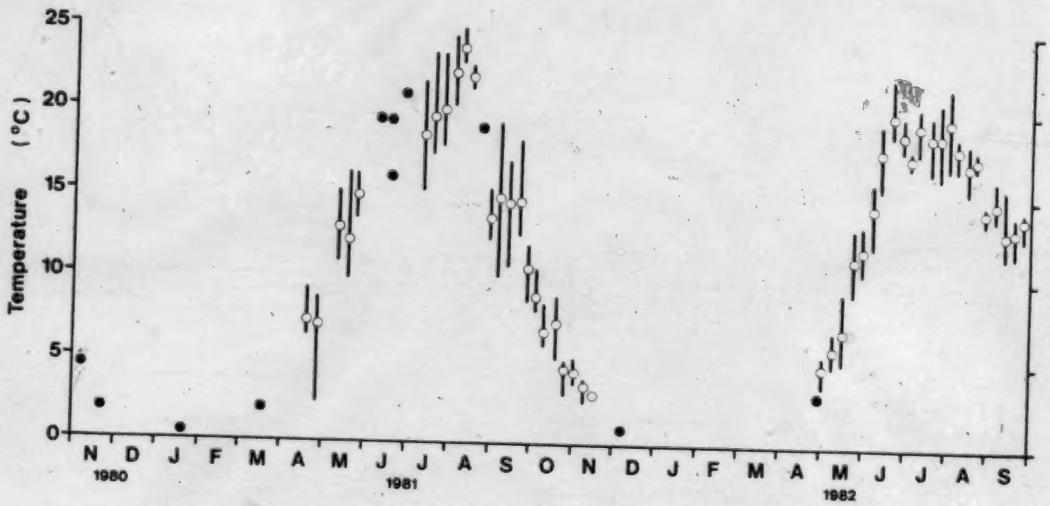

Figure 2. Water temperatures of the Sturgeon River during the sampling period. Mean weekly temperatures and their ranges are shown for most of the year; black dots indicate single temperature readings.

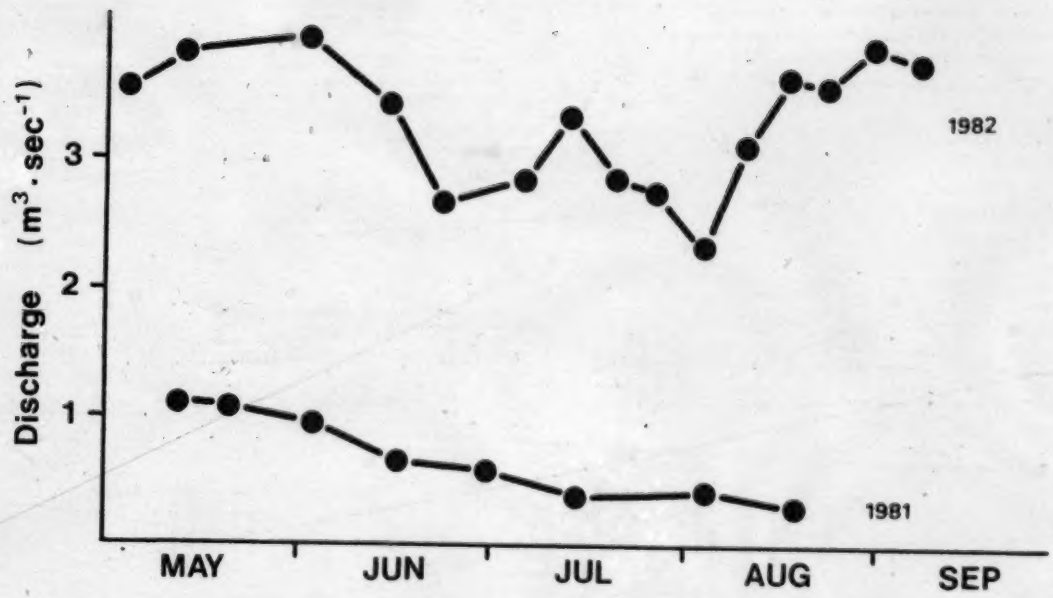

Figure 3. Estimates of discharge ($m^3 \cdot s^{-1}$) in the Sturgeon River at the outlet of Lac Ste. Anne during the summers of 1981 and 1982.

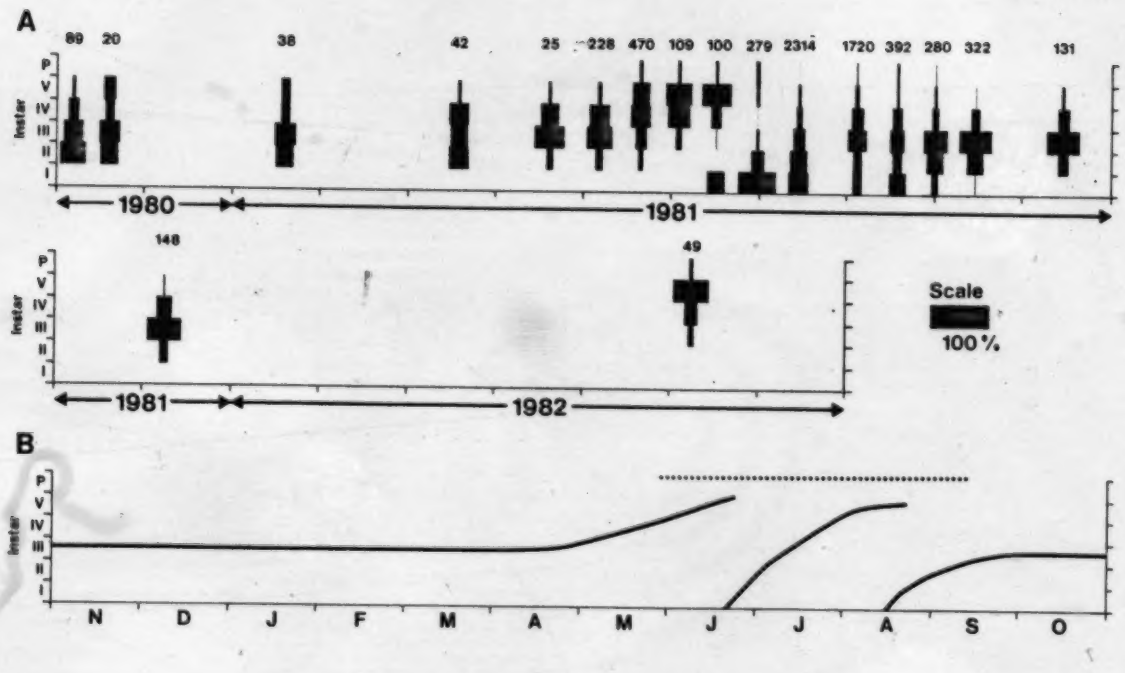

Figure 4. Life cycle of *Neureclipsis bimaculata* in the Sturgeon River from November 1980 to June 1982. A. Histograms represent relative percentage of total individuals in each stage. Numbers over the histograms are the sample sizes. P includes prepupae and pupae. B. Schematic life cycle based on mean stage at each sampling date. Dotted line represents adult flight period.

were present on all sampling dates until 31 August. First instar larvae were first collected on 15 June and were present in all samples until 14 September. No first instar larvae were found in samples during autumn, winter, or early spring.

There was considerable overlap between the two generations and very little synchrony of development within a cohort. The first individuals to emerge from the summer generation appeared in mid-July 1981.

The life cycle was consistent during both winters. However in June 1982 the progress of the winter generation lagged behind what had occurred the year before. No individuals had pupated by 7 June 1982; whereas in 1981 pupae were common by that date.

In 1981, adults were collected throughout the sampling period (Figure 5). The last adult collected was a male that emerged between 4-14 September. In 1982, males were first captured between 14-17 June and females between 17-21 June. Emergence peaks occurred at the end of June (winter generation) and the middle of August (summer generation) in both 1981 and 1982 (Figures 4 and 5). Males appeared before females in all generations sampled (Figure 5). The winter generation was completed by the middle of July in both years.

The nets that the larvae build were conspicuous in the river. In 1981 the first nets were observed on 19 May. Nets became more numerous as the summer progressed, but

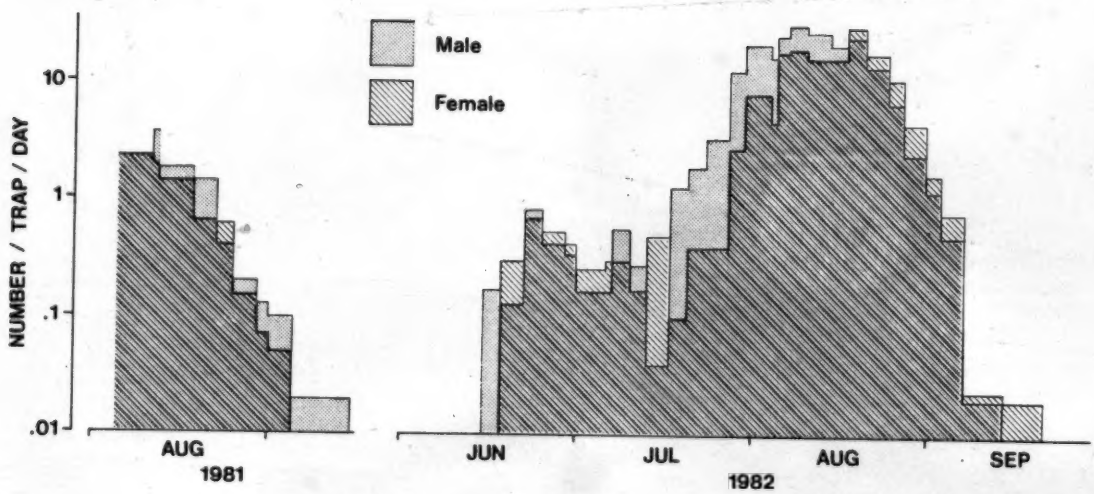

Figure 5. Emergence phenology of *Neureclipsis bimaculata* adults captured in floating traps on the Sturgeon River. Males shown by stippling, females by crosshatching. Note logarithmic scale for numbers/ trap/ day.

began to decrease sharply in number during the last week of August. A few small nets (of early instar larvae) were observed until the middle of September. All larval instars construct filtering nets (Brickenstein 1955). During autumn, winter and early spring, larvae did not build capture nets, but maintained a small retreat tube of silk similar to the retreat portion of the capture net. In 1982 the first appearance of nets was not until 12 July. Based on emergence records, the 1982 life cycle phenology was about a week behind that of 1981.

Pupae of *N. bimaculata* usually swim until they encounter an object suitable for crawling up before they eclose. Pupae do not eclose on contact with the surface in midstream.

A large proportion of larvae were infected with a gregarine protozoan parasite. Rates of infection ranged from 50-100% in samples examined. These protozoans were found in their sporadin stage between the peritrophic membrane and gut wall. A cyst-like protozoan seen along the lateral areas of the abdomen of almost all L-IV and L-V larvae was probably the sexual stage of the same gregarine seen along the larval guts. Gregarines are apparently common in Trichoptera larvae. In a survey of Italian Trichoptera, 39 of 71 species checked had gregarines; but of the three polycentropodids, none had gregarine parasites (Moretti and Sorcetti 1981).

Microdistribution

Since the distribution of larvae was significantly non-random, with variance:mean ratios greater than one, i.e. clumped (X^2, $p<0.05$) in all instars on all dates (except for very few instances), abundance data were log(n+1) transformed before analysis. The different instars were considered separately for the analysis to test for instar specific patterns of distribution. Sampling dates were considered separately to avoid complications due to phenology of *N. bimaculata* or aquatic macrophytes or other environmental variables. Data were analyzed with product moment correlations (Sokal and Rohlf 1981) and a multiple regression computer package (BMDP, University of California).

Chara sp. and *Potamogeton richardsonii* were the predominant aquatic macrophytes during the study period. *Potamogeton* grew from tubers beginning in May and died during autumn, while *Chara* covered about the same relative amount of bottom area throughout the sampling period (Figure 6). The apparent increase in *Chara* abundance late in the season may represent its underestimation in samples when it was obscured by the dense *P. richardsonii* population. *Myriophyllum exalbescens* and *Potamogeton pectinatus* populations were common but did not cover much of the total area sampled; both were seasonal in abundance, being present only during the summer and autumn. Since *Equisetum* and *Typha latifolia* populations were only in

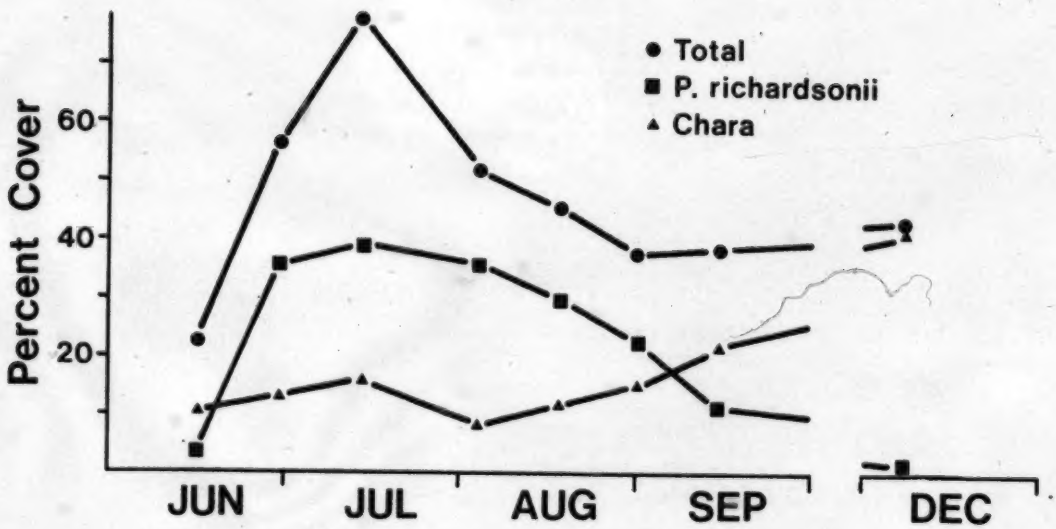

Figure 6. Seasonal phenology of *Chara* sp., *Potamogeton richardsonii* and total plants based on percentage cover in samples.

marginal areas, they rarely occurred in samples.

Densities of *N. bimaculata* larvae in each instar were often positively correlated with total plant cover (Table 3). Of the different macrophytes, *Chara* and *P. richardsonii* had the most number of significant associations with *N. bimaculata* densities. The only significant association with *Myriophyllum exalbescens* was a negative correlation with density of L-IV larvae. Although *Equisetum* specimens were rare in samples (covering a mean of 2.3% in 3 out of 20 samples), it was positively correlated with densities of L-I and L-IV larvae and total density on 15 June 1982. There were only a few significant correlations between current velocity and *N. bimaculata* density (Table 3). Density of larvae tended to be positively correlated with depth except for the negative correlation between first instar larvae and depth on 3 August.

On most dates, the numbers of the different larval instars were positively correlated with each other ($p<0.05$). There were no significant negative correlations, which might have suggested some microhabitat differentiation between instars. Densities of prepupae and pupae were rarely correlated with larval instars other than L-V.

Population Dynamics

Population estimates were characterized by high variance. On all sampling dates the numbers in most instars

Table 3. Table of significant product moment correlations between densities of *Neureclipsis bimaculata* and microhabitat variables.

Date (d·m) 1981	Total Plant Cover	*Chara*	*P. r.*[1]	*Equisetum*	*M. e.*[2]	Current	Depth
19·05							+LIII* +P*
15·06		-LIV*	-LI* +PP* +P*	+LI* +LV* +TOT*			
29·06	+LV**		+P*			-LV* -PP*	
13·07							+LIV* +LV*
03·08	+LI* +LIII* +LIV** +LV** +PP*	+LI* +LIV** +LV*	+LIV* +LV* +PP** +P**			+LI* +LII* +LIII*	-LI*
17·08	+LIII* +LIV* +LV*		+LV*				+LIV* +LV* +PP* +P*
14·09			-LIV*		-LIV*		
07·12	+LII* +LIII* +LIV*	+LII* +LIII** +LIV* +TOT**					

[1] *Potamogeton richardsonii*
[2] *Myriophyllum exalbescens*
* $p<0.05$
** $p<0.01$

had variance to mean ratios significantly greater than one (X^2, $p<0.05$). The highest density recorded was 1171 individuals in 945 cm^2, or 12391 $\cdot m^{-2}$ (see Appendix 1).

Larval densities of the winter generation were only about 15% of those of the summer generation in 1981 (Figure 7). The winter generation appeared to increase in abundance over the course of the winter and early spring, before the beginning of the emergence period. However, this is an artifact of the small number of samples (n=5), since data from core samples suggests that density decreased over winter (Appendix 1). The summer generation reached its peak density on 13 July 1981 and began decreasing again as the adults of this generation began emerging. The population declined sharply during middle and late August.

Larval densities of L-IV, L-V, and total individuals (including prepupae and pupae) over the study period showed two distinct peaks, one for each generation, in early May and mid-July (Figure 7 and Appendix 2).

Emergence trap data for 1982 also indicated two peaks (Figure 5). But emergence data as a population estimate may be biased since pupae may swim to the traps as a convenient object to crawl onto prior to eclosion. Emergence data showed that the summer generation was 55.4X more numerous than the winter generation in 1982. The large increase in the numbers of summer generation adults collected in 1982, relative to 1981, might be due to a minor modification I made to the trap nets in 1982 (the addition of a cloth

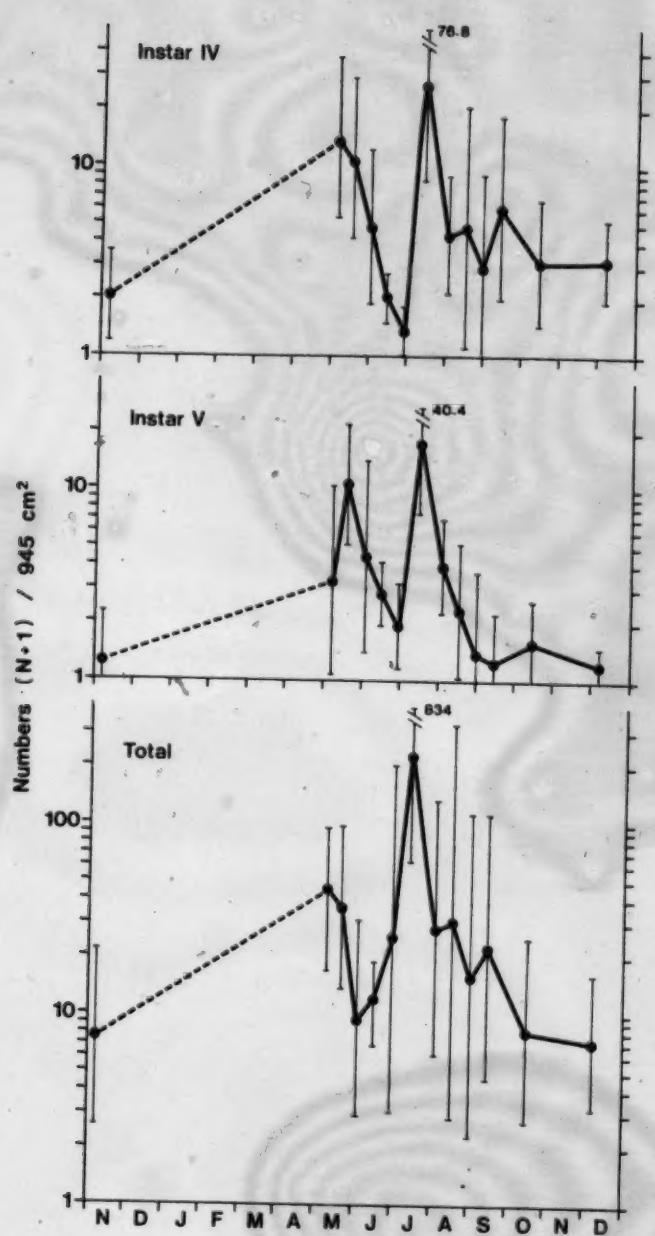

Figure 7. Population estimates of *Neureclipsis bimaculata* for larval instars IV and V, and total individuals (including all larval instars, PP and P) from benthic samples. Geometric means ±95% confidence intervals. Note logarithmic scale.

flange along the bottom). However, the large number of adults observed flying in the field and the large number of pupae (pharate adults) swimming about in the river in 1982 were not noted in 1981. The numbers of adults collected in emergence traps in 1982 were 127 (winter generation) and 7040 (summer generation). The sex ratio was not different from unity in the winter generation ($X^2=1.32$, $p>0.1$, 1d.f.), but males were significantly more numerous than females (1.36:1 males:females) in the summer generation ($X^2=163.2$, $p<0.001$, 1d.f.).

Production was estimated using the instantaneous growth method (Waters 1977). Annual production for the *N. bimaculata* population in the Sturgeon River for 1981 was calculated to be 3.58 g dry wt$\cdot m^{-2} \cdot yr^{-1}$ (Table 4). Approximately 74% (2.66 gm) was contributed by the summer generation. Ash content of larvae was 4.25%, making ash-free production 3.43 g$\cdot m^{-2} \cdot yr^{-1}$. Turnover ratios (production/ $\bar{X}$ biomass) were 5.25 for the winter generation and 6.41 for the summer generation. Note that calculations for the winter generation were based on parts of two different cohorts.

Discussion

Life History

Larval growth and instar data indicate a bivoltine life cycle for the *N. bimaculata* population in the Sturgeon River. The bimodal nature of the emergence data and the

Table 4. Production estimate calculations according to the instantaneous growth method.

Date (d·m·y)	MIW† (mg)	Standing Crop /945cm²	Growth	Mean Standing Crop	Production
06·11·80	0.24	2.03			
			0.74	12.30	9.11
05·05·81	0.49	22.57			
			0.87	44.21	38.41
19·05·81	1.18	65.84			
			0.35	45.10	15.65
02·06·81	1.67	24.36			
			0.37	22.13	8.12
15·06·81	2.41	19.89			
	(0.005)‡	(0.019)			
			0.17	14.25	2.49
			(1.22)	(0.44)	(0.54)
29·06·81	2.87	8.62			
	(0.017)	(0.86)			
			(2.75)	(51.51)	(141.66)
13·07·81	(0.27)	(102.16)			
			(0.86)	(87.29)	(75.42)
03·08·81	(0.63)	(72.42)			
	0.019	1.19			
			(0.43)	(45.06)	(19.69)
			1.04	2.13	2.22
17·08·81	(0.98)	(17.70)			
	0.054	3.07			
			(1.17)	(11.48)	(13.41)
			0.92	4.59	4.24
31·08·81	(3.16)	(5.27)			
	0.14	6.12			
			0.25	7.87	1.94
14·09·81	0.17	9.62			
			0.81	8.02	6.52
15·10·81	0.39	6.43			
			-0.33	5.12	-1.67
07·12·81	0.28	3.80			
				16.57	87.05
				(39.16)	(250.99)
			$\bar{X}$=	30.12	338.03

† Mean Individual Weight
‡ All values in brackets are for summer generation
Note: all values based on an area of 945 cm².

population estimates also support this interpretation. However, the variation in developmental stages within a cohort and the resulting overlap of cohorts during the late summer make it difficult to readily distinguish the two generations. Longer intervals between sampling would have obscured a bivoltine interpretation of the life cycle.

This is the first detailed study of a *Neureclipsis bimaculata* population in North America. Robertson (1967) made observations on the life cycle of a *N. bimaculata* population in the Wandering River, Alberta, where it leaves Lyle Lake. Based on monthly sampling and with relatively few larvae, he concluded that the population was univoltine in the Wandering River. Robertson also noted the wide range of sizes present throughout the year. All other work on this species has been reported from the Palaearctic. Wesenberg-Lund (1911) suggested that *N. bimaculata* had a 2-year life cycle in west Denmark, but gave no reason for this conclusion. He may have based this on the wide range of sizes of larvae present at most times of the year. Alm (1926) also reported a 2 year life cycle in Sweden based on the large variation of larval sizes found in late November. Statzner (1979) accepts Alm's interpretation of a 1 to 2 year life cycle. However, Statzner's data are not incompatable with a bivoltine life cycle interpretation. Tachet and Bournaud (1981) recently described a *N. bimaculata* population as univoltine in France. In Bavaria, populations of this species have been reported to

have two flight periods suggesting bivoltinism (Brickenstein 1955). The flight period is quite long (2-4 months) in most regions (Wesenberg-Lund 1911, Nimmo in press). Whether European populations have a bivoltine life cycle cannot be resolved satisfactorily from available data. Perhaps *N. bimaculata* populations are capable of flexibility in the duration of the life cycle as has been reported for some other caddisflies (e.g. Gotceitas and Clifford in press).

Estimates of degree day accumulations in the Sturgeon River for the summer generations of *N. bimaculata* amounted to 1270 and 930 degree days in 1981 and 1982 respectively, and 1500 degree days for the winter generation 1981 to 1982. The annual degree day accumulation in the Wandering River was about 2525 (calculated from data in Robertson 1967) and an average of 4360 for the Rhône River, France (calculated from data in Tachet and Bournaud 1981). Even if there is a threshold temperature for growth, both the Wandering River and Rhône River sites provide warm enough conditions for *N. bimaculata* to be bivoltine. From this I conclude that either temperature is not the most important variable determining apparent voltinism of *N. bimaculata* or these workers misinterpreted their life cycle data. If temperature is not of paramount importance then one must look elsewhere for environmental conditions influencing voltinism. *Pletrocnemia conspersa* (Curtis) (Polycentropodidae) populations can complete the life cycle at different rates depending on both temperature and food

supply (Tachet 1967). As will be discussed in the next section, productivity of the lake feeding a stream and resulting seston loads may play a part in determining voltinism.

The sex-related size dimorphism of instar L-V head widths may account for the six larval instars attributed to this species by Brickenstein (1955). This bimodal distribution of L-V head widths has recently been shown to be a sex-related size dimorphism in other caddisfly species, e.g. *Odontocerum albicorne* (Scopoli) (Elliott 1982) and *Dicosmoecus atripes* (Hagen) (Wiggins and Richardson 1982).

Adult males appeared in the population about a week before females. There was no significant difference in growth rates between the sexes (see chapter 2). The longer time for females to reach maturity is probably due to the fact that they reach a weight 3.4 times that of males and therefore take longer to mature. Perhaps the significantly lower number of females in the summer generation of 1982 represents extra mortality during this extra time as larvae.

Observations on the seasonality of net spinning by *N. bimaculata* larvae in European streams (Wesenberg-Lund 1911, Brickenstein 1955, Statzner 1979) are similar to those of the Sturgeon River study. Wesenberg-Lund (1911) found a few nets in December when the lake that was the source of his stream was ice-covered. Net building is strongly affected by current. As current velocity increases, smaller and smaller nets are

constructed; eventually they cannot be made to withstand the current (Brickenstein 1955). In the Sturgeon River, net construction apparently started much later in 1982 than in 1981. This may be attributed to the higher discharge and accompanying greater current velocities in 1982. Once aquatic macrophytes were large enough to impede the current, *N. bimaculata* nets began to appear. Henri Tachet (personal communication) collected large numbers of *N. bimaculata* larvae at certain sites in the Rhône River only during years of low discharge and low current velocities. Other filter feeding caddisflies have also been reported not to spin nets during winter under ice cover (Fuller and Mackay 1980). Some species of *Hydropsyche* switch to grazing instead of filter feeding during the period when they do not maintain nets (Fuller and Mackay 1980). I have no data on winter feeding by *N. bimaculata* larvae.

Most populations of zooplankton reach their maximum density between April and October, particularly cladoceran populations (Hutchinson 1967, Armitage and Capper 1976). The seasonal periodicity of net building by *N. bimaculata* corresponds well with the seasonal density fluctuations of limnetic zooplankton species. The onset and end of net building by *N. bimaculata* larvae in the Sturgeon River occured when the water temperature was close to 10 to 12°C. If the increase in zooplankton numbers is as strongly temperature related as has been suggested (Pennak 1978) then temperature may be an important proximate cue to net

construction. This would be an interesting problem to approach experimentally.

Microdistribution

The importance of plants as a substrate for the larvae of *N. bimaculata* is apparent from my study. Plants provide a substrate to which larvae can attach their capture nets and retreat tubes. By attaching to plants, such as *P. richardsonii* and *Equisetum* sp., etc, and deadfall branches, larvae are able to utilize the entire cross-section of the river. Also, flow is reduced nearer the river bottom as a result of the dense growth of macrophytes; this forces larvae to situate higher in the water column to filter sufficient food material. During the large part of the year when larvae do not spin nets, they are found attached to plants such as *Chara* and any other structures to which they can attach their retreat tubes. The advantage of attaching to *Chara*, which maintains its holdfast over winter, is obvious since most other plants die back and *Chara* provides one of the few microhabitats available in winter. Also, much of the river bottom is severely scoured by the breakup of ice and subsequent spring runoff. Therefore, there is a strong seasonal component to the use of available substrates by *N. bimaculata* larvae. Statzner (1978, 1979) demonstrated the importance of substrates that allow direct access to the water column, by using bamboo poles as artificial substrates. Wesenberg-Lund

(1911, 1943) reported that *N. bimaculata* larvae were dense on plants such as *Potamogeton* and gave some illustrations of net form. My results are similar to those reported in Wesenberg-Lund's work.

Statzner (1979) described the importance of clumps of shells of *Dreissena polymorpha* (Pallas) (Pelecypoda) in providing suitable substrate for *N. bimaculata* larvae to attach their nets. Removing all *Dreissena* specimens significantly reduced *N. bimaculata* densities (Statzner 1979). The larvae have also been reported to live under or between stones in faster flowing water than found in the Sturgeon River (Brindle 1960, Armitage 1976). Although there were some areas of stone and gravel bottom in the Sturgeon River, very few *N. bimaculata* larvae were collected in these areas.

The influence of current on the distribution of *N. bimaculata* larvae has been commented on previously (Brickenstein 1955). In one study, larvae colonized artificial substrate baskets of stones in currents up to 60 $cm \cdot s^{-1}$, although most larvae were found in slower water (Armitage 1976). Current velocities in the Sturgeon River in 1981 were almost always less than 20 $cm \cdot s^{-1}$ and usually less than 10 $cm \cdot s^{-1}$. Larvae of *N. bimaculata* were found in abundance even in slow-moving marginal areas where currents were less than the detection limits of the current meter (about 5-6 $cm \cdot s^{-1}$). Given the range of current speeds reported for *N. bimaculata*, there was not a wide enough

range of current velocities in the Sturgeon River to determine current speed preferences. Wallace *et al.* (unpublished manuscript) noted an inverse relationship between the size of the capture net and current velocity in Sweden. Thus, the high discharge and accompanying fast currents in the Sturgeon River in 1982 may have been responsible for the delay in net-building observed.

Population Dynamics

The sudden decline in numbers of larvae in late August, 1981, suggests that the lower density in the winter generation is not primarily a result of mortality over the winter. A number of hypotheses related to reduction in available substrate and delayed hatching of eggs may be proposed to explain this phenomenon, as outlined below.

The winter generation appears as the vegetation dies back; hence less substrate is available and young larvae may be more vulnerable to predation than during summer. This could affect population sizes. This hypothesis could be tested by artificially increasing available substrate.

If Robertson's (1967) hypothesis that there is continuous or delayed hatching of *N. bimaculata* larvae is correct, then perhaps a large proportion of the population overwinters as eggs. Statzner (1979) reported finding first instar *N. bimaculata* throughout the autumn and winter in Germany. Also, other polycentropodid populations are thought to have continuous hatching, e.g. *Polycentropus*

flavomaculatus (Pictet) (Elliott 1968) and *Plectrocnemia conspersa* (Edington and Hildrew 1981). The apparent increase of *N. bimaculata* larvae during winter in my study is the result of small sample sizes. The numbers of larvae from core samples during this period showed a decrease in numbers through the winter. Thus, density estimates and the absence of first instar larvae, except in summer, suggests there is no continuous hatching in this population of *N. bimaculata*. This is in contrast to the findings of Statzner (1979).

The increase in the *Neureclipsis* population size from 1981 to 1982 might have been a result of higher water levels and greater discharge in 1982 (once current velocities were slow enough to permit net construction). The increase in depth would provide a greater cross-section of river which larvae could occupy. The higher discharge also would provide greater total amounts of seston for these filter feeding larvae.

The production value (3.58 $gm \cdot m^{-2}$) for the *N. bimaculata* population in the Sturgeon River is higher than reported for most caddisflies, although by no means the highest (Waters 1977, Benke and Wallace 1980). Cudney and Wallace (1980) reported values up to 18.2 $g \cdot m^{-2} \cdot yr^{-1}$ for a *Cheumatopsyche pasella* Ross population, in the Savannah River of the southeastern United States.

General Discussion

There are two other common, widespread species of *Neureclipsis*, *N. crepuscularis* (Walker), and *N. valida* (Walker). A population of *N. crepuscularis* in the Savannah River, U.S.A. was bivoltine (Cudney and Wallace 1980). The larvae of this population were found mostly in current velocities from 10 to 25 $cm \cdot s^{-1}$ which is similar to the range of current speeds where *N. bimaculata* larvae are found. The capture net of *N. crepuscularis* larvae is like that of *N. bimaculata* (Cudney and Wallace 1980, J.B. Wallace -personal communication). Information on *N. valida* is scarce, but the larvae appear to live in stronger currents than *N. bimaculata*. *Neureclipsis valida* has been reported from the Montreal River, Saskatchewan, Canada (Cushing 1963, personal communication) and waveswept shorelines of South Indian Lake, Manitoba, Canada (D.M. Rosenberg -personal communication).

Apparent differences in voltinism of *N. bimaculata* throughout its range need to be considered relative to environmental factors other than degree day accumulations, because temperature alone would not appear to account for the differences. It would be interesting to consider how temperature influences net building of *N. bimaculata* and its relation to population growth of zooplankton species. The hypothesis that voltinism may be more closely related to productivity of the source lake (than to, for example, temperature) should be considered.

Experimental manipulation of microhabitats may be necessary to understand fully the importance of certain plant types to microdistribution. These manipulations should also be designed to detect seasonal shifts in larval microdistribution, which seem to occur. One pattern not investigated was the height above the river bottom that larvae occupy. This will obviously be related to the phenology of the plants used as substrate, but will also likely show that larvae occur higher in the water column during summer than at other times. Some sort of manipulation or artificial substrate design would improve the estimates of relative population numbers, although to do this one needs to consider seasonal changes in microhabitat utilization.

CHAPTER TWO

Seston dynamics and their influence on the growth and distribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) larvae in a boreal river, Alberta.

Introduction

For several years freshwater ecologists have been interested in the abundance, and longitudinal patterns of abundance, of invertebrates (especially filter feeders) downstream of lakes and reservoirs. Changes in seston type and abundance have been studied by a number of workers (Chandler 1937, Reif 1939, Maciolek and Tunzi 1968, Carlsson *et al*. 1977) as have variations in the abundance of invertebrates downstream of lakes (Müller 1954, Illies 1956, Cushing 1963, Oswood 1979). Most filter feeding organisms reach maximal densities immediately below lake outfalls, with abundance decreasing exponentially downstream (Sheldon and Oswood 1977). A number of adult aquatic insects fly upstream until they encounter a lake and then oviposit in the outflow area, and this can account for high densities of larvae in lake outflow streams (Müller 1954, 1982). Müller (1954) considered a "lake outlet community" as distinct from other lotic communities.

Some filter feeding invertebrates are largely restricted to lake and reservoir outflows. Some common filter feeders decrease in numbers downstream of a lake outlet, while others, such as larvae of certain simuliids

and *Neureclipsis bimaculata* (L.) usually disappear entirely a short distance downstream of lakes (Carlsson *et al.* 1977, Edington and Hildrew 1981, Statzner 1979). Obviously, some unique combination of ecological factors restricts distribution of these populations.

Some of the characteristics of lake outflow reaches of streams that change downstream include (1) type and abundance of seston (suspended particulate matter) including silt load, (2) short-term variation in discharge, and (3) daily temperature variations. Also, lake outflows tend to be wide and shallow, providing relatively more laminar flow (Armitage 1976, Carlsson *et al.* 1977). Many authors have mentioned that lake-produced seston is a potential food source (rich with live algae and zooplankters) for stream invertebrates. However, little work has been done on the seston dynamics and the importance of changes in seston quality on the growth of filter feeding invertebrates. Carlsson *et al.* (1977) suggested that lake outlet seston concentrations of particles greater than 2 μm in diameter were not the major influence on the abundance of simuliids at lake outlets. Statzner (1978) stated that the abundant planktonic drift at lake outflows was of minor importance to the distribution of *N. bimaculata* larvae.

I studied aspects of the seston dynamics from a lake outlet stream in central Alberta, Canada. Experiments were designed to test the effect of seston changes on growth of *N. bimaculata* larvae. Particularly, I wished to test the

hypothesis that seston type and abundance are important determinants of the distribution of *N. bimaculata* larvae at lake outfalls. In addition, alternate hypotheses for, and apparent exceptions to, this pattern of distribution are considered.

Study Area

The Sturgeon River is a slow moving, third order stream of the boreal forest region, draining into the North Saskatchewan River. The section of river considered in my study flows out of Lac Ste. Anne, and enters Matchayaw ("Devil's") Lake about 25 km downstream (53°43' N, 114°15' W) (Figure 8). The river descends at an average gradient of about 2.1 $m \cdot km^{-1}$ between the two lakes. Six sites on the river were studied during 1982. Two sites were studied in detail and these are referred to as the "Lake" and "Onoway" stations (Figure 8).

Materials and Methods

Water samples for seston analysis were collected either by a van Dorn bottle from a bridge, or by immersing water bottles by hand. Known volumes of water were filtered through preashed Whatman GL/C filters. Filters were dried (50°C, 24 hrs.), weighed (Mettler AK160, to nearest 0.1 mg), ashed (550°C, 1 hr.), rewetted (to restore water of hydration), dried and weighed. To separate seston into size fractions, the wet filtration method of Gurtz *et al.* (1980)

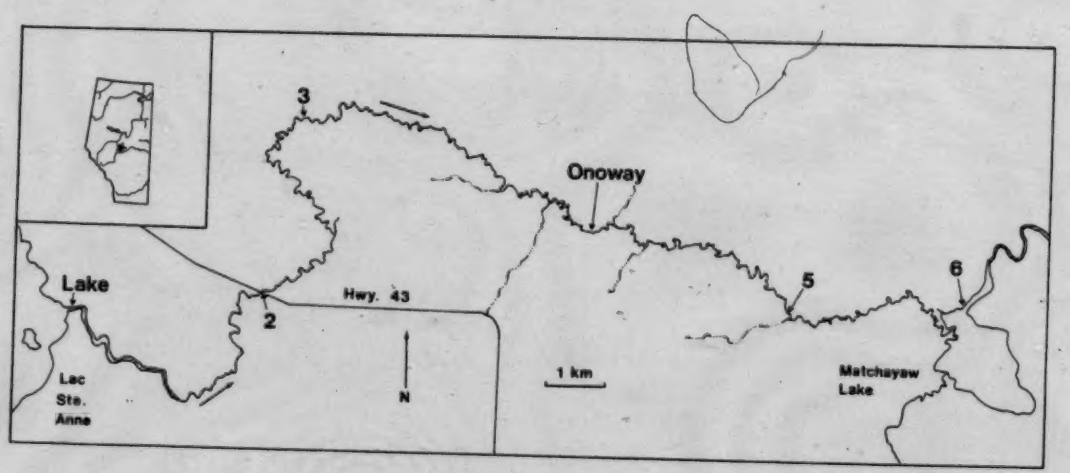

Figure 8. Map of the Sturgeon River in the study area. The six sampling stations are identified by numbers except for the Lake and Onoway sites. Inset map of Alberta shows location of study area.

was used.

To study the effect of seston source (i.e. lake outlet or a downstream site) on growth, fifth instar *N. bimaculata* larvae were collected, transported to the laboratory and separated into males and females on the basis of head width (see Chapter 4). Larvae were blotted, weighed and each placed in a separate marked cage (described below). To avoid having individuals begin metamorphosis during an experiment, only male larvae below 15 mg (wet weight) and females below 35 mg were used. This threshold weight was determined so that experimental animals weighed at least 3 to 5 mg less than the smallest prepupa of each sex.

The cages were cylinders (7 x 3 cm) of Nitex® screening with mesh opening of approximately 1.0 mm. These cylinders were capped at each end with another piece of screening fastened with silicone sealant. About four or five meshes of one end were cut so that larvae and food could be inserted, but the nylon meshes were close enough together to close off exit to the larvae.

For the laboratory experiments, seston was collected from each of the two field sites, Lake and Onoway. Seston was collected using a plankton net with mesh opening of 80 µm, at 36 hour intervals to account for variation in quality or quantity of seston and to maintain a fresh supply of food for the larvae. The concentrated seston from each of these two sites were the two feeding treatments.

In the first experiment, 12 larvae (6 of each sex) were randomly assigned to each of two laboratory streams, which were in a controlled environment room (20°C, 15L:9D photoperiod). Larvae were allowed 24 hrs to spin nets inside their cages. Seston, either from the Lake or Onoway station, was then placed into the larval nets by means of a pipette inserted into the opening of the cage. Large amounts of seston (such that food material remained in the net at the next feeding) were added to the net of each larva at least four times a day on an irregular basis. After 8 days, larvae were removed, blotted and weighed again.

In a second laboratory experiment, 10 polystyrene containers (29x18x13 cm) were used. Each was supplied with an air bubbler to create a slight current. One male and one female larva were weighed and placed in each tank. The tanks were randomly assigned to the two feeding treatments. As in experiment 1, larvae were fed concentrated seston by means of a pipette inserted in the front of the net. After 8 days, larvae were reweighed and preserved.

Another group of *N. bimaculata* larvae were placed in polystyrene containers and fed 30-40 *Daphnia pulex* Leydig per day for 8 days. In all laboratory experiments, feeding was ended 12 hours before the larvae were reweighed.

In a field experiment, female larvae were randomly assigned to two groups of 10 larvae each, wet weighed and placed into cages as in experiment 1. These 10 cages per treatment were attached to wooden stakes, and one stake per

treatment (10 cages) was placed at each of the two field sites (Lake and Onoway stations). An attempt was made to choose locations with similar mean current (25 $cm \cdot s^{-1}$), depth (75 cm) and lighting (unshaded). After 8 days these cages were recovered and larvae again wet weighed and preserved.

Individual growth rates were calculated by the instantaneous growth rate (IGR) equation

$$(1) \quad IGR = \frac{\log W_2 - \log W_1}{t}$$

where W_1=initial weight.
W_2=final weight.
t=time in days.

For all treatments, percent weight increase was calculated by

$$(2) \quad \text{Relative Growth} = \frac{W_2 - W_1}{W_1} \times 100\%.$$

All experiments were carried out between 10 August and 2 September 1982.

Results

Seston Dynamics

There were marked seasonal changes in seston concentrations leaving Lac Ste. Anne (Figure 9). Values during the early half of the summer were lower than those during the last half of July through August. At the lake

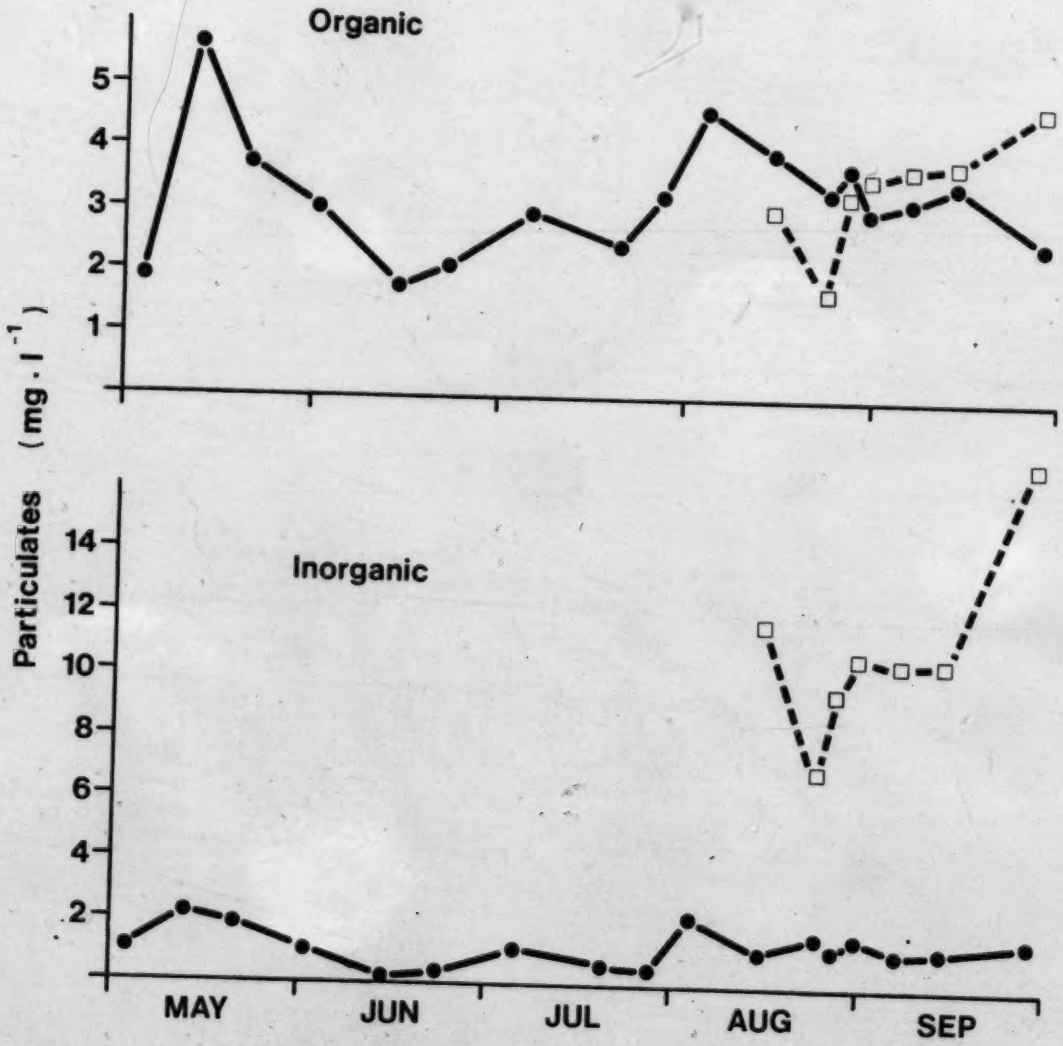

Figure 9. Seasonal seston dynamics at the outlet of Lac Ste. Anne (closed circles, solid line) and Onoway (open squares, dashed line). Upper graph is the organic component (OPM), lower graph is the inorganic component (IPM). Note difference of scale between graphs.

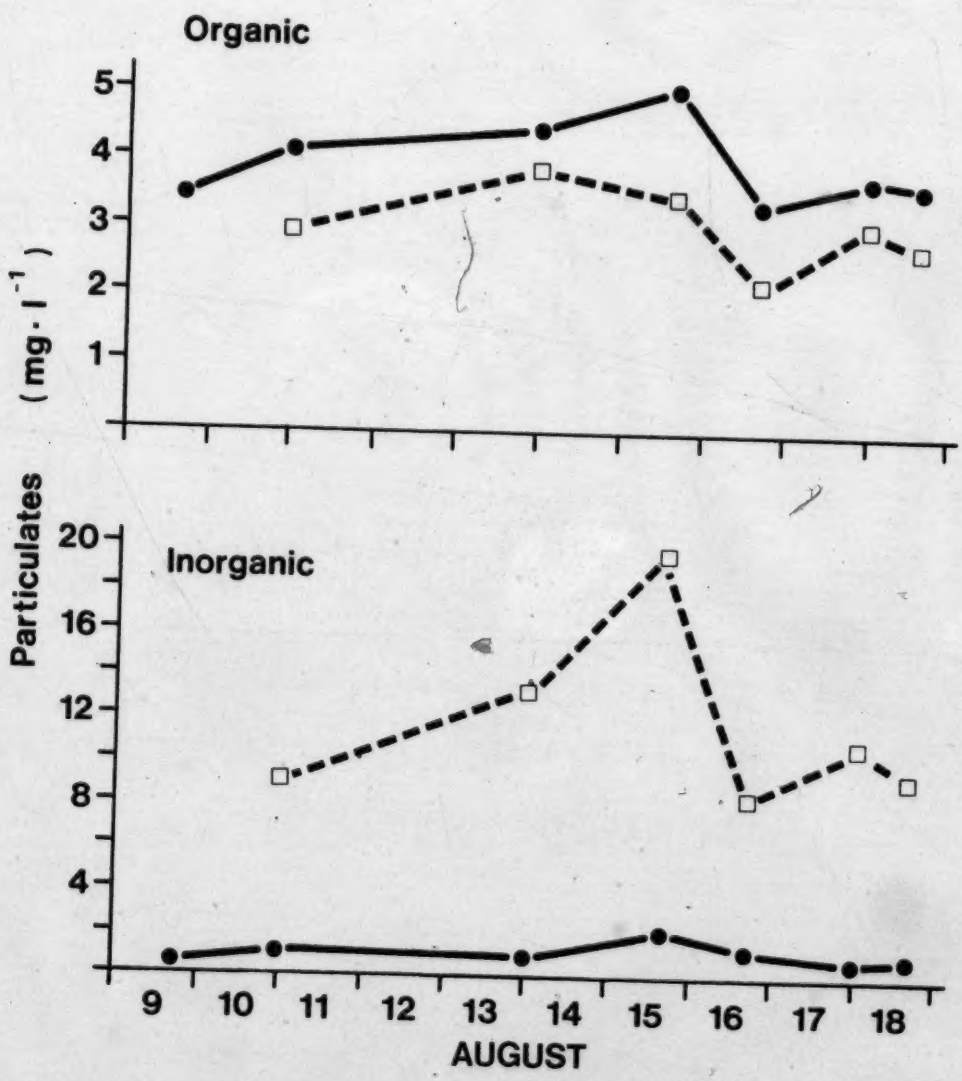

Figure 10. Seston dynamics for a 10-day period in August 1982 showing short-term fluctuations. In Figure 9 these data are combined in one point per curve. Symbols as in Figure 9.

outlet (Lake station), the inorganic fraction of the seston was always less than the organic portion and usually less than 30% of total seston. At the Onoway station, the situation was reversed with the inorganic component very high and the organic portion usually less than one-third of total seston. The seston load at Onoway varied more between sampling trips than the load at the lake outlet, largely due to the inorganic fraction. These differences were obvious from day to day (Figure 10).

Seston was divided into four size fractions. The amount in each size fraction was variable between sampling dates. The size fraction less than 63 μm usually made up more than 50% of the total weight of seston. Particles more than 250 μm consistently made up the smallest proportion of the four size categories (Figure 11). Suspended particulates tended to be larger at the lake outlet than at the Onoway station.

Concentrations of organic particulate matter (OPM) were relatively constant at the downstream sites, although seasonally variable at the lake outlet (Figures 9 and 10). Inorganic particulate matter (IPM) increased with increasing distance downstream, but decreased significantly (t-test, $p<0.05$, 4 df) immediately downstream of Matchayaw Lake (Figure 12).

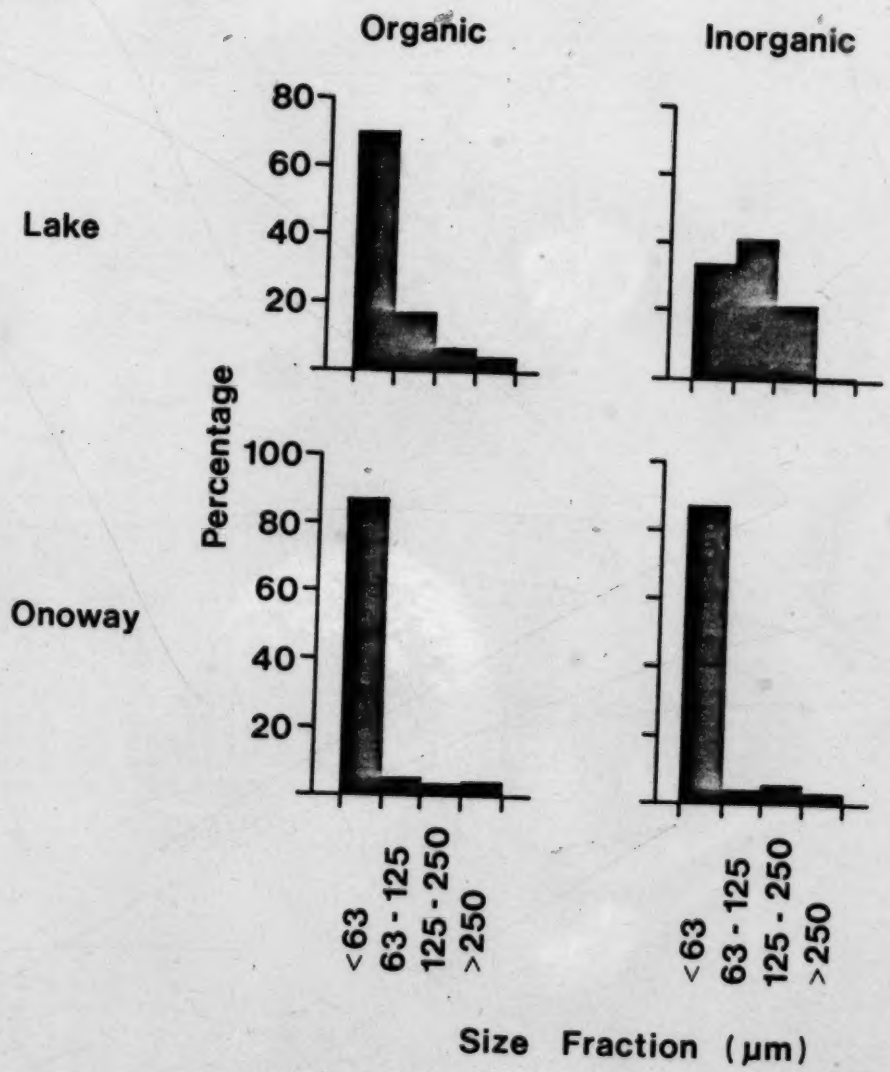

Figure 11. Percentage composition of particulate matter in transport, Sturgeon River. Mid-day samples collected 17 August 1982 (Lake), and 13 August 1982 (Onoway).

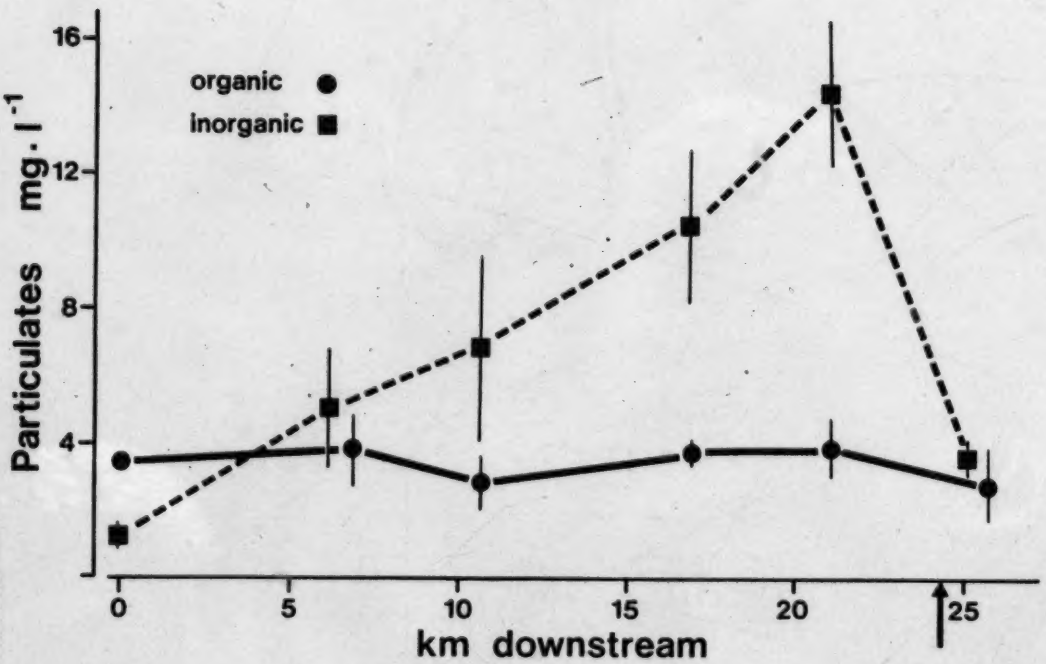

Figure 12. Downstream changes in particulates in the Sturgeon River between Lac Ste. Anne and Matchayaw Lake (denoted by arrow). Six points correspond to six sampling stations shown in Figure 8. Means ±95% confidence intervals.

Growth Rates

The instantaneous growth rates of a group of larvae fed live *Daphnia* did not deviate significantly from zero when plotted against mean individual larval weight (ANOVA, $p>0.05$, $n=21$). Therefore size-related differences in growth could be ignored.

In laboratory experiment 1, two larvae began pupation and two other larvae died. These animals were disregarded, reducing the sample size in certain treatments. The instantaneous growth rate was calculated for remaining individuals and tested by a 2-way ANOVA (BMDP computer package, University of California). Growth varied significantly both between seston treatments ($p<0.0001$, 1 d.f.) and between sexes ($p<0.001$, 1 d.f.). There was no significant interaction ($p>0.05$). The relative weight changes for each treatment are shown in Table 5. Note the high variance of the relative weight changes within treatments.

In the second laboratory experiment, all larvae spun nets of sizes similar to those seen in the field. During this experiment a total of three animals died (one-lake seston treatment, two-Onoway seston treatment). In this experiment, the difference in growth rate between sexes was not significant ($p>0.05$, 1 d.f.), but the difference between stations was highly significant ($p<0.0001$, 1 d.f.). As in experiment 1, larvae in the Lake treatment grew faster than larvae in the Onoway treatment (Figure 13).

Table 5. Percent increase in individual wet weight of *Neureclipsis bimaculata* larvae after 8 days of feeding under experimental conditions. Means ±standard error and N.

Laboratory Experiment 1.

	male			female		
Onoway	14.8	±33.7	5	2.7	±2.7	6
Lake	69.4	±152.7	5	23.1	±70.8	4

Laboratory Experiment 2.

	male			female		
Onoway	0.2	±2.2	4	3.7	±14.5	4
Lake	58.3	±29.2	4	69.0	±159.0	5

Field Experiment.

Onoway			Lake		
-2.5	±3.6	7	10.1	±34.7	6

Daphnia.

male			female		
97.5	±253	6	67.1	±58.5	14

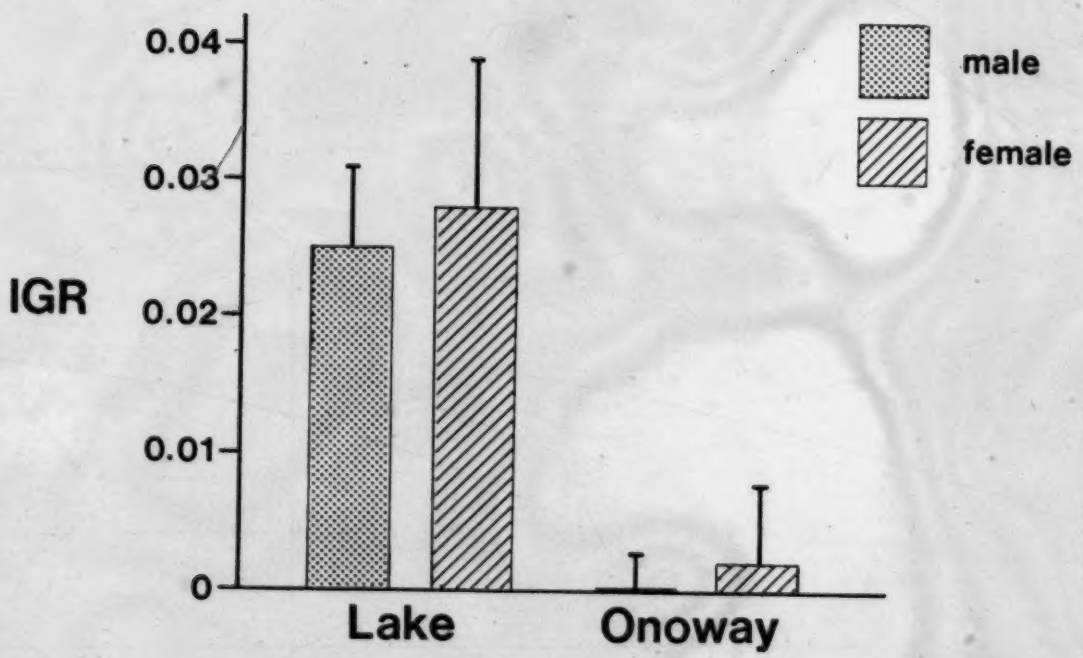

Figure 13. Results of laboratory experiment 2 showing differences in the instantaneous growth rate of larvae fed one of two types of seston. Means ±95% confidence intervals.

In the field experiment, only females were used. Seven of the initial 20 animals (4 from lake site, 3 from Onoway site) were unaccounted for. Presumably they escaped via the small hole made for insertion. All cages containing animals had definite nets inside them. Growth of *N. bimaculata* larvae at the lake outlet was significantly greater than at the Onoway site (t-test, $p<0.05$, 11 df) (Figure 14).

There was no significant difference in the growth rates of male or female larvae fed *Daphnia* (t-test, $p>0.2$, 19 df). The growth rates of larvae fed seston from the lake station in laboratory experiment 2 were not significantly different from those of larvae fed pure diets of *Daphnia* (males $t=2.12$, 8 df, $p>0.05$, females $t=0.33$, 18 df, $p>0.1$).

Discussion

Seston changes and growth of *N. bimaculata*

Seston values obtained in this study are within the normal range of values found in other studies of seston dynamics (Sedell *et al.* 1978). The short-term variation in seston loads is probably the result of different processes at the two sites. At the lake outlet the differences are presumably due to the different types and numbers of organisms being carried out of the lake relative to season, temperature, light, precipitation, discharge, wind, etc. At the downstream site, runoff is probably of most immediate importance in influencing seston dynamics.

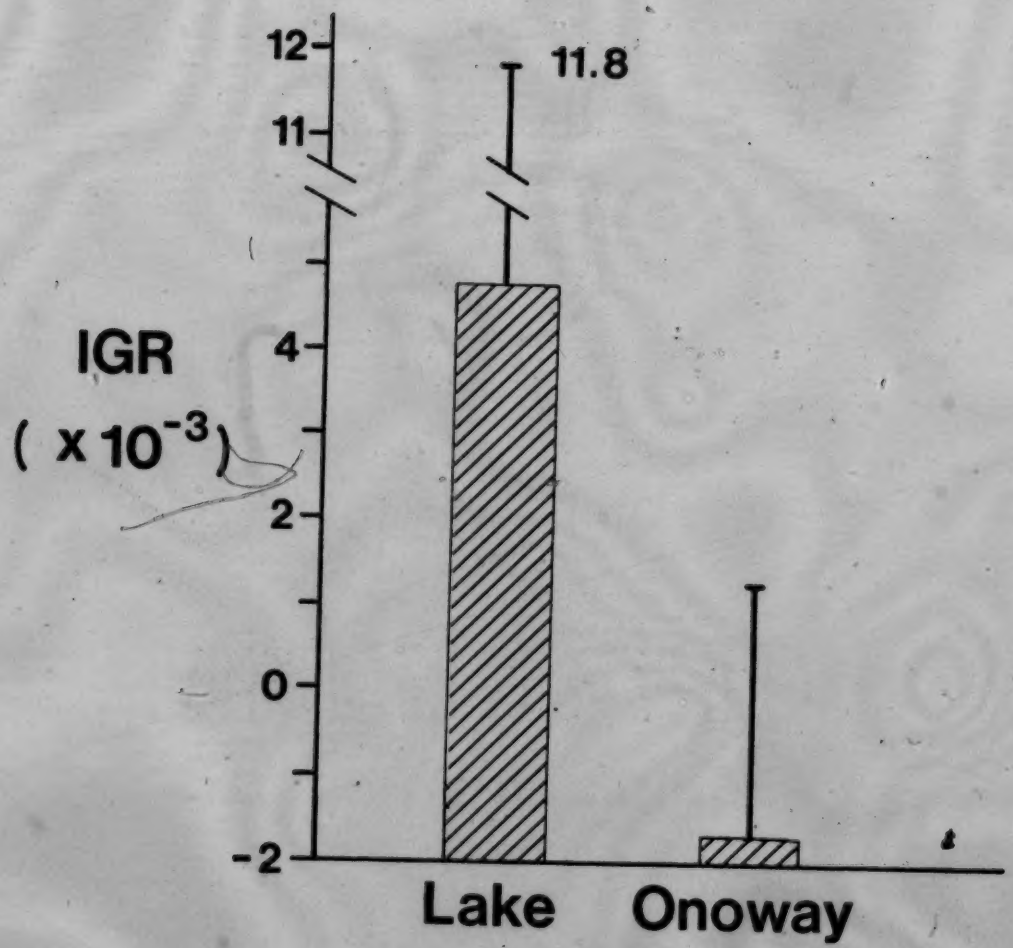

Figure 14. Results of the field experiment showing the instantaneous growth rates of larvae. Means ±95% confidence limits.

There was a moderate decline in the concentration of organic seston downstream from the lake and a large increase in the inorganic fraction. Seston samples from the lake contained large amounts of algae, as well as copepods and cladocerans, whereas samples from Onoway had mostly detritus particles, fine sand and silt. A comparison of the chlorophyll *a* concentrations at each of the two sites on 9 September, 1982, showed that the Lake seston had a concentration 2.5 times that of the Onoway seston. The difference is likely greater during the summer, since algae populations were already dying back when these samples were taken. The large inorganic component of seston at Onoway seems characteristic of the Sturgeon River. This agrees with the general observation that lakes act as sinks for silt (Armitage 1976).

The results of the experiments reported here reveal that seston quality is very important in determining the growth of larval *N. bimaculata*. Even though larvae were fed in excess of what they could ingest, there was negligible growth for animals fed seston collected 17 km downstream of the lake. In fact, many larvae lost weight on a diet of seston from the Onoway site. However, larvae of *Hydropsyche* and *Cheumatopsyche* were both common at the Onoway site, and these filter feeders apparently survive on the seston from that site. This supports the hypothesis that seston quality, not quantity of OPM, determines growth in *N. bimaculata* larvae. Seston quality may be affected by

large concentrations of IPM, which could clog filtering nets or reduce OPM intake by larvae. Experiments to test this could be easily performed by adding ash to lake-derived seston.

I used only fifth instar larvae and assumed that earlier instar larvae would show similar patterns of growth on the two types of seston. Early instar hydropsychid larvae have been shown to feed more heavily on detritus than later instar larvae (Benke and Wallace 1980, Fuller and Mackay 1981). But, Fuller and Mackay (1981) have demonstrated that third and fourth instar *Hydropsyche* spp larvae grow faster on animal and diatom food than on detritus. Even if early instar *N. bimaculata* larvae can grow on a diet of natural detritus (similar to that in Onoway seston), I predict growth on a diet of lake outlet seston would be as high or higher than that on a diet of detritus.

Growth in terms of rate or percent increase was variable within treatments. Part of this variation may be a result of differences in the amount of water within each larva, since water content is known to change with physiological and developmental condition (Chapman 1969). Correlation between wet weight and dry weight of *N. bimaculata* larvae was significant (males $r=0.9$, $n=22$, $p<0.01$, females $r=0.9$, $n=22$, $p<0.01$), but only accounted for 80% of the variation between these two variables.

The significant difference between growth of male and female larvae in the first laboratory experiment was not observed in subsequent experiments. It is possible that "cage effects" may have been important since the cages were smaller than the normal size of a net made by female larvae in similar currents, and this may have interfered with normal feeding.

The growth rates attained on diets of *Daphnia* or seston from the lake source can be considered maximal rates. The gain in wet weight was very high, attesting to how rapidly *N. bimaculata* larvae can develop. Fuller and Mackay (1981) reported maximum increases of 32% for larval wet weights in *Hydropsyche sparna* Ross, 26% for *H. betteni* Ross, and 15% for *H. slossonae* Banks, when fed enchytraeid (Oligochaeta) worms for 14 days. These increases for *Hydropsyche* larvae are much lower than the increases obtained by *N. bimaculata* larvae in only 8 days. However, the *Hydropsyche* experiments were conducted at 10-12°C while the *N. bimaculata* laboratory experiments were at about 20°C. This difference makes direct comparison tenuous.

The abundance of filter feeding organisms is usually maximal immediately below lake outlets (Cushing 1963, Hynes 1970, Oswood 1979). The explanation usually given for this is that large amounts of high quality seston support more individuals. As one goes downstream from the lake source this food resource is processed, reducing its quality and therefore accounting for lowered densities of these filter

feeding organisms downstream (Benke and Wallace 1980). Most of these organisms can also be found any distance downstream of a lake source (within certain ecological constraints), although in smaller densities (Cushing 1963, Oswood 1979). However, *N. bimaculata* larvae are not usually found beyond distances of 1.5 km below lake outfalls (Illies 1956, Statzner 1979, personal observation). Rarely, a few individuals are found downstream, but these are likely individuals that have drifted from the main population.

Effects of seston quality

While many workers considered seston quality to affect primarily population density, only recently have studies of seston quality on individual growth appeared in the literature (Ward and Cummins 1979, Fuller and Mackay 1981). If the numbers of living organisms in the seston is an indicator of seston quality, then quality declines rapidly with distance from a lake outlet (Chandler 1937, Maciolek and Tunzi 1968, Sheldon and Oswood 1977). If the decline in individual growth of larvae downstream is nearly proportional to this seston quality, then *N. bimaculata* larvae drifting and settling further downstream would experience lower growth rates than conspecifics upstream. Lower growth will mean longer time to complete development, increasing chances of mortality, and slowing population growth. Even if these "downstream" larvae can complete development, they may have less energy to put into egg

production and thus lower potential fitness. This would certainly place a strong advantage on remaining near the lake outlet. Carlsson *et al.* (1977) found that simuliid larvae had lower growth rates with increasing distance downstream from a lake outlet. While other factors undoubtedly influence the distribution of *N. bimaculata* larvae, the effect of seston type on individual growth suggests that it is a primary determinant of distribution and presumably abundance.

Larvae of *N. bimaculata* do occasionally drift, but drift distances have not been measured (Statzner 1979). Statzner (1978) has shown that adult *N. bimaculata* fly upstream to oviposit at the lake outlets. This behaviour, for aquatic insects in general, has been considered as compensation for drift (Müller 1954, 1982). The advantage of this is obvious if an individual's offspring grow better nearer the lake outlet.

My results suggest that seston quality greatly influences the growth of *N. bimaculata* larvae. Given the importance of an individual's proximity to the source of high quality seston, then populations of *N. bimaculata* should reach their highest abundance at lake outlets due to the availability of a high quality food source.

Other patterns of population distribution

Larvae of *N. bimaculata* have also been collected along lake shores and inflow streams where lake and stream water

mix (Hickin 1967). These examples do not contradict the hypothesis that seston quality affects distribution, since larvae would still have this rich food source available. D.M. Rosenberg (personal communication) has collected larvae of *N. bimaculata* along certain areas of the shores of South Indian Lake in northern Manitoba, Canada, where constant but gentle wave action provides flow necessary to push lake water through the larval nets. Tachet and Bournaud (1981, H. Tachet- personal communication) found *N. bimaculata* larvae in the Rhône River where current velocity slowed to 20-40 $cm \cdot s^{-1}$. Popowa (1927) collected larvae throughout the Volga River system, but the larval guts were filled mostly with algae and remains of typical zooplankters. Larger rivers tend to have seston of higher quality, as determined by higher algal counts (Naiman and Sedell 1979). These observations do not necessarily contradict the hypothesis that seston quality affects distribution.

Effects of seston on life history

The effect that seston quality has on the life cycles of filter feeding animals has not been widely considered. There is evidence to suggest that *Hydropsyche* populations below an impoundment in Southern Ontario, Canada, are bivoltine, whereas populations of the same species elsewhere on the same river are univoltine (Mackay 1979). Tachet (1967) experimentally determined that food supply and temperature both have a significant effect on the time it

took a *Plectrocnemia conspersa* (Curtis) population to complete its life cycle. If higher quality seston allows faster growth, then perhaps apparent variation in voltinism of *N. bimaculata* populations may be explained by productivity of the source lake (see chapter 1).

Several European workers have suggested that *N. bimaculata* populations may have a univoltine or semivoltine life cycle in localities in Denmark (Wesenberg-Lund 1911), Sweden (Alm 1926),northern Germany (Statzner 1979) and France (Tachet and Bournaud 1981). Perhaps these populations occur below less productive lakes than Lac Ste. Anne, where *N. bimaculata* was bivoltine. Wallace *et al.* (unpublished manuscript) have found that larval weight of three populations of *N. bimaculata* was positively correlated with lake productivity. Certainly the effect of lake productivity on voltinism would be an interesting hypothesis to explore.

There were no apparent temperature differences in the Sturgeon River between the sites sampled. Carlsson *et al.* (1977) found temperatures in a Swedish lake outlet stream site were intermediate between temperatures at two downstream sites. Temperature, in terms of degree days, seems of minor direct importance to the overall growth of *N. bimaculata* larvae (see Chapter 1). In my laboratory experiments, temperature was controlled and therefore differences in growth rate were not affected by temperature.

Other factors affecting distribution

Other factors may influence the density and distribution of *N. bimaculata* populations. Carlsson *et al.* (1977) have commented that the geomorphology of lake outflow stream reaches tends to be wide and shallow, providing relatively more laminar flow. The importance of turbulence to the function of the fragile net of *N. bimaculata* is obvious from observation of larvae in laboratory streams. Fluctuations in current speed (e.g. from 10 to 2 $cm \cdot s^{-1}$) can result in the net collapsing. Once collapsed, a net does not return to its original form (personal observation). Thus, degree of turbulence may also influence the distribution of *N. bimaculata* larvae. Tachet (personal communication) suspects that distribution of *N. bimaculata* larvae is primarily determined by current velocity. The influence of current velocity and turbulence on distribution needs to be determined experimentally.

The sites where *N. bimaculata* larvae have been collected without being associated with lake or reservoir outflows tend to be large rivers (Popowa 1926, Lepneva 1964, Tachet and Bournaud 1981). When tests of the river continuum hypothesis consider higher order rivers, it would be worthwhile to attempt bioassays of growth rates of filter feeding animals on seston from rivers of different magnitude. In addition, the influence of the system's productivity on voltinism and adult size needs to be tested.

Growth rates of larval *Neureclipsis bimaculata* are strongly affected by the source of the seston on which they feed. In low order streams (orders 2 and 3) seston quality is highest in lake outlet reaches and *N. bimaculata* larvae are rarely found far from the lake. However, in higher order rivers (where p/r tends to be >1), such as the Volga and Rhône Rivers, the larvae of *N. bimaculata* seem to be found along the course of these rivers irrespective of lake outlets.

CHAPTER THREE

The feeding behaviour of *Neureclipsis bimaculata* larvae (Trichoptera: Polycentropodidae).

Introduction

The distribution of organisms is often determined by the availability of certain resources. An adequate food supply is one resource which can potentially limit distribution. Among freshwater filter feeding invertebrates, distribution may be influenced by seston type and abundance (Mackay and Wiggins 1979, Alstad 1982). In the past some authors have concluded that quantity of organic seston is not a limiting resource in many rivers, but quality may be (Georgian and Wallace 1981).

The filter feeding larvae of *Neureclipsis bimaculata* (L.) (Polycentropodidae) occur almost exclusively at the outflows of lakes and reservoirs (Statzner 1979, Edington and Hildrew 1981). Guts of these larvae contain a range of food types, including larvae of aquatic insects (chironomids, mayflies, etc.), and coarse detritus, but predominantly small crustaceans (Copepoda, Cladocera) and algae (Popowa 1927, Lepneva 1964, Wiggins 1977, personal observation). This suggested that one possible hypothesis to account for their restriction to lake outflows is that larvae might have a well-defined response to certain prey types.

In order to test this hypothesis, the feeding behaviour of larval *N. bimaculata* in artificial laboratory streams was observed in response to different types of particles intercepted by their filtering net. The questions addressed were:

1. Are there different responses to certain prey types?
2. Do larvae respond differently to living versus dead animals?
3. Is there evidence to suggest that *N. bimaculata* larvae are specialists and only incidentally take other kinds of food items?

Materials and Methods

Live larvae were collected during July and August from the Sturgeon River where it flows out of Lac Ste. Anne, Alberta, and transported in river water to the laboratory. Care was taken not to crowd larvae since they will injure and even kill conspecifics, as in *Plectrocnemia conspersa* (Curtis) (Hildrew and Townsend 1980). Larvae were placed in an artificial laboratory stream, powered by a paddlewheel (current velocity approximately 10 to 12 $cm \cdot s^{-1}$), filled with dechlorinated water in a controlled environment room (photoperiod 15L:9D). Temperature was maintained at 20°C. The laboratory stream had plexiglass sides to facilitate observation. A piece of screening on the stream bottom provided larvae with a suitable substrate for attachment. Larvae were left for 24 hrs to construct

nets. Experiments began 24-48 hrs after larvae were first collected. Individuals were identified by letters written on the outside of the plexiglass.

The capture net of *N. bimaculata* is a relatively large, silken structure consisting of three parts (Figure 15). Details of the size and shape of the net are variable, being influenced by larval instar, current velocity, and substrate form (see Brickenstein 1955). The retreat is the narrow posterior portion where the larva resides most of the time. It is the only portion of the net that is maintained year round in the field. The large anterior end is referred to as the funnel. The middle portion, which is where the net makes a sharp bend, is known as the drop zone. A detailed analysis of net construction has been presented by Brickenstein (1955).

A range of potential prey types were tested which might be encountered by larvae in the field (Table 6). Most of these prey items were collected fresh in the field with the exception of *Daphnia pulex* Leydig, which were from a laboratory culture. In addition, white worms (Oligochaeta: Enchytraeidae) and dry fish food flakes were tested. The three main treatments were chironomid larvae (Orthocladiinae), and live and dead (killed in hot water, approximately 60°C) *Daphnia pulex*.

Particles were dropped into the entrance of the capture net by means of a pipette, with special care taken not to contact the net or create extra water movement. Movements

Table 6. Summary of objects inserted into the net of *N. bimaculata*.

Prey or Food Type	Number of Trials	Number Captured or Taken
Daphnia pulex (live)	32	27
Daphnia pulex (dead)	23	16
Chironomidae (Orthocladiinae 5-10 mm long)	29	11
Hyallela azteca (4-10 mm long)	12	0
Leptophlebia cupida (9-12 mm long)	10	0
Caenis sp. (5-8 mm long)	10	0
Enchytraeidae (approx. 20 mm long)	15	15
Dry fish food	6	0

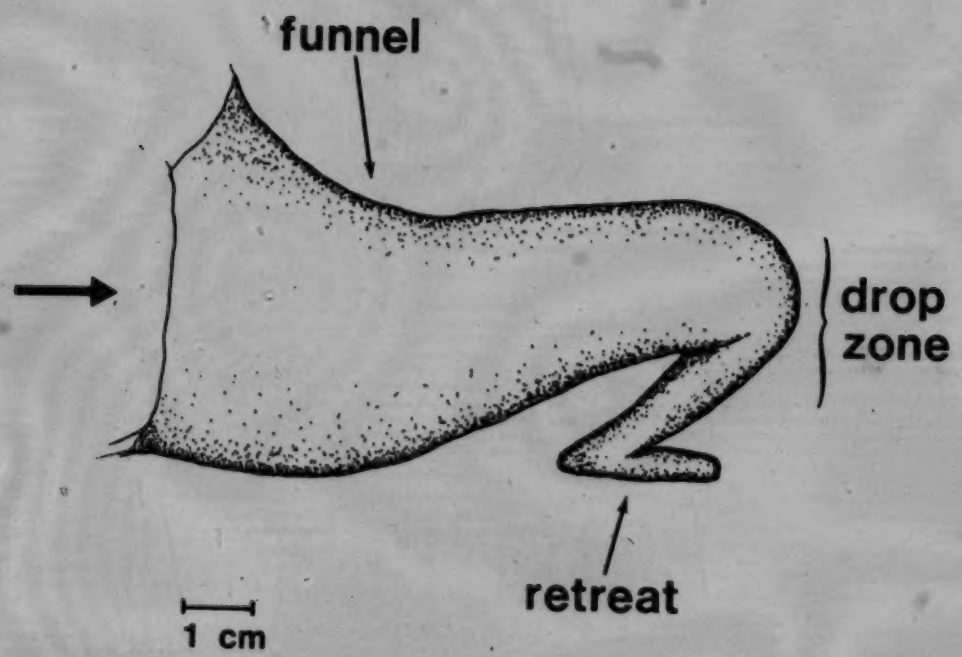

Figure 15. The capture net of a fifth instar *Neureclipsis bimaculata* larvae showing component parts. Arrow indicates direction of flow.

of larval *N. bimaculata*, from the first impact of the particle on the net were recorded and timed. Individual larvae were observed for no more than 15 minutes for each trial. For any set of experiments, each individual received each treatment only once, to avoid experience effects. When a larva received more than one treatment, the order was randomized and at least 12 hours allowed between trials. A prey item was recorded as "taken" or "captured" when the *N. bimaculata* larva was able to begin to feed within the 15 minute observation period. Among the information recorded was the position on the capture net where the prey item became ensnared, response distance (distance from particle where larva began to "search" actively), response time (time from particle impact on the net, to capture), and number of lost contacts (when a larva made contact with the particle and left it again apparently without feeding). The term "net disturbance" is used to indicate the impact of an object on the net or vibrations induced by that object.

Results and Discussion

Behaviour

Tachet (1971) identified seven behavioural stages in the feeding response of *Plectrocnemia conspersa* larvae (Polycentropodidae) from a resting position. These same stages observed in *N. bimaculata* are (1) arousal (2) displacement (moving forward into the drop zone), (3) capture, (4) retreat with prey, (5) manipulation,

(6) ingestion, and (7) preening (which Tachet 1971 referred to as "la toilette"). I observed the following generalized response to prey landing in the capture net. Initially the larva lifts its head from the prognathous resting position and begins to move as an object hits the net. If the disturbance is intense the larva moves to the back of the retreat; otherwise it moves out towards the drop zone. Upon encountering a prey item the larva usually uses a quick ventrad movement of the head to knock the prey against the mesh of the net. Then it would grab the prey with its mandibles and rapidly drag it back to the retreat. In the retreat or drop zone the larva secretes silk to help immobilize the prey, and uses the prothoracic legs and mouthparts to manipulate the prey. After feeding, the remnants of the prey, e.g. the carapace of Cladocera, remain fastened to the wall of the drop zone or retreat tube. Eventually the larva spins a new portion of web over it and the old bits of net eventually slough off. All this is similar to that reported for *P. conspersa* (Tachet 1971).

Feeding Experiments

Some prey types introduced into the mouth of the net were consistently able to escape by crawling or swimming out of the net, and they were never captured by *N. bimaculata* larvae in these experiments (Table 6). These animals were the amphipod, *Hyallela azteca* (Saussure), and nymphs of *Leptophlebia cupida* (Say) and *Caenis* sp. (Ephemeroptera).

Flakes of dry fish food elicited no response and in some instances remained tangled in the silk of the funnel for several days. Enchytraeid worms (Oligochaeta) introduced into the nets were always captured and eaten within about ten minutes.

There was no significant difference in the capture success of live or dead *Daphnia* (2x2 contingency, $X^2=1.75$, $p>0.05$) (Table 6). However, both live or dead *Daphnia* were captured significantly more frequently than chironomids (2x2 contingency: live *Daphnia*- $X^2=14.1$, $p<0.005$, dead *Daphnia*- $X^2=5.25$, $p<0.05$). Many of the chironomid larvae were able to escape without difficulty by crawling between the meshes of the silk net. Once a live *Daphnia* was inside the funnel of the net, it would attempt to swim against the current and end up being carried to the posterior end of the net where it was quickly captured. Dead *Daphnia* were usually rolled to the back of the net by the water current (although sometimes this occurred after the 15 minute observation period, and therefore was not counted as captured in table 6).

Response by *N. bimaculata* larvae is related to where the potential prey item contacts the net. These results showed that *N. bimaculata* larvae responded more often to prey landing in the retreat than in the drop zone and more often to prey in the drop zone than in the funnel (Table 7). This suggests that larvae are only sensitive (or at least responsive) to items touching the net close to them.

Table 7. Number of responses to prey landing in different parts of the capture net.

Part of Net	No. of Trials	No. of Responses
Retreat	28	28†
Drop Zone	29	22
Funnel	13	0

†Differences between response frequencies in different parts of the net significant (Fisher's Exact Test, $p<0.005$).

One time I watched a *N. bimaculata* larva attempt to capture a small, vigorously moving air bubble, trapped in the drop zone of its capture net, for 30 minutes. Tachet (1977) was able to stimulate the prey response in larvae of *Plectrocnemia conspersa* by applying mechanical vibration to the net. Thus, tactile cues are important in eliciting the prey response. Chemosensory cues are not likely to be important to *N. bimaculata* larvae, but cannot be ruled out as a possibility.

Response distance, although crudely measured, is an estimate of sensitivity to net disturbance. Larvae of *N. bimaculata* had a greater response distance to chironomids and live *Daphnia* than to dead *Daphnia* (Mann-Whitney U-test, $p<0.05$ and $p<0.005$, respectively). There was no significant difference in response distance between live *Daphnia* and chironomid larvae (Mann-Whitney U-test, $p>0.05$). Response distances ranged from zero to 8 mm, but were usually less than 4 mm (Figure 16). Prey items, especially *Daphnia*, were often swept to the *N. bimaculata* larva by the current.

Response times of *N. bimaculata* larvae (see Appendix 3) were significantly shorter for live *Daphnia* than either dead *Daphnia* or chironomids (Mann-Whitney U-test, $p<0.001$ for both tests). There was no significant difference between the response time to dead *Daphnia* and chironomids (Mann-Whitney U-test, $p>0.05$). The long response time to chironomids was due to these prey items clinging to the net and crawling about, rather than being swept immediately to

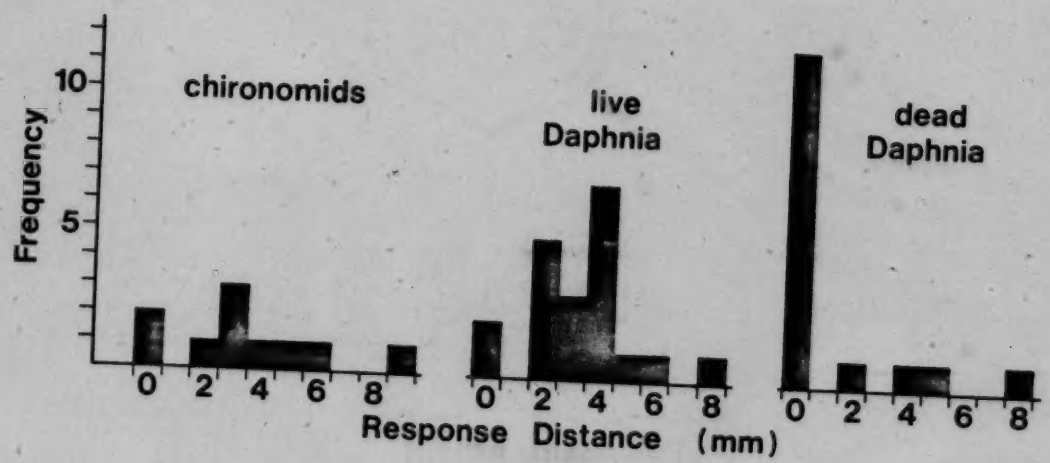

Figure 16. Frequency of response distances to different food types.

the drop zone or retreat. Dead *Daphnia* would often land in the drop zone and elicit no response from larval *N. bimaculata* (see section on response distances). The response of *N. bimaculata* larvae to objects in the net seems to be more a function of prey size and activity in the net than a prey-specific response.

Observations of conspecifics entering the net of another *N. bimaculata* larva, showed that the resident larva went through the same initial behavioural sequence as for prey interception. The resident larva crawled forward into the drop zone and either lunged at the intruder (as in Hildrew and Townsend's , 1980, agonistic encounter of *Plectrocnemia conspersa*), or retreated suddenly. These observations are preliminary, but suggest that the size of the intruder may be important in determining the outcome. Intruders that are larger than residents were often able to chase the resident from the net and take the net over. This has also been shown for *P. conspersa* larvae (Hildrew and Townsend 1980).

Tachet (1977) showed that response distance in *P. conspersa* was a function of amplitude and frequency of the disturbance. *N. bimaculata* larvae react only to large intruders in the funnel portion of the net, such as conspecifics. Intruders in the drop zone, which were the size of small chironomids and *Daphnia*, elicit an attack response.

Larvae must have some tactile mechanism to detect prey on the capture net. Jansson and Vuoristo (1979) have shown that *Hydropsyche* larvae have a mechanism by which they can detect stridulation of congeneric larvae. This mechanism may involve the use of setae on the legs as vibration receptors and apposition of one or more legs to the net. A similar mechanism may be used by *N. bimaculata* larvae to sense prey vibrations on the net. Although Jansson and Vuoristo (1979) considered these receptors to be important for receiving stridulation vibrations from congenerics, they may have a far greater significance. Larvae of *Hydropsyche* and *Cheumatopsyche* have been shown to eat a large proportion of animal material (Benke and Wallace 1980, Fuller and Mackay 1980). These vibration receptors may be used by many filter feeding caddisfly species to detect prey in their nets. Philipson (1953) reported that larvae of *Hydropsyche instabilis* Curtis kept in laboratory aquaria, siezed prey items very rapidly when they were intercepted by the net. He noted in contrast that larvae use side-to-side head movements to clean the net, and presumably check for food particles. I suggest that a vibration detection response to prey may have evolved in the Hydropsychoidea, since many other invertebrate organisms use such a response, e.g. many spiders, and Chaetognatha (Horridge and Boulton 1967).

Neureclipsis bimaculata larvae do not appear to exhibit prey-specific responses. Rather, the larvae exhibit a generalized response pattern to disturbance of the net.

However, since many potential prey items are able to escape from the net, lake outflows (with their abundant zooplankton) provide a good source of easily trapped prey. It seems that even though the feeding response of *N. bimaculata* larvae is very general, the capture net has evolved to be efficient at capturing a limited variety of prey items. The similarity in the feeding behaviour sequence of *N. bimaculata* and *Plectrocnemia conspersa* larvae suggests that this may be a generalized feature of larvae in this family. This hypothesis remains to be tested.

In short, the prey response of *N. bimaculata* larvae appears to be a general response to disturbance of the net. The function of the net seems to have evolved to be efficient at trapping only a small range of prey types and sizes. Thus, the specialization to prey types is not in the larval response, but in the functional design of its capture net. Therefore, the distribution of of *N. bimaculata* populations may be influenced by availability of easily caught prey items in the seston.

CHAPTER FOUR

The determination of a sex-related size dimorphism in larvae of *Neureclipsis bimaculata*.

Introduction

Organisms often exhibit sex-related differences in morphology, physiology and behaviour. Considerations of sex-specific differences in life history or distribution is rare for immature insects, because sex cannot generally be determined except for later stages of most hemimetabolous insects. Since the immature stage is the longest part of the life cycle in most aquatic insects, including Trichoptera, an examination of sex-related differences is important.

The sex of larval caddisfies cannot generally be determined. Females of many species are larger than males, but the size differences of larvae are not reliable or distinct enough. A number of workers have noted the large size difference between male and female imagos of *Neureclipsis bimaculata* (L.) (Brickenstein 1955, Brindle 1960, personal observation). My data show that the dry weight of female pupae of *N. bimaculata* is 3.4 times that of male pupae. From this, I suspected that the strongly bimodal head width frequency distribution of fifth instar larvae might be sex-related.

Methods and Materials

Fifth instar larvae of *N. bimaculata* were measured across the head at the level of the eyes to the nearest 0.024 mm. In addition, maximum length (FCL) and width (FCW) of the frontoclypeal apotome (FCA) was measured for many of the larvae (Figure 17). Since the sex of pupae can be accurately determined and larval sclerites remain in the pupal cell, the frontoclypeal apotomes of pupae from field collections were also measured. The size distributions of frontoclypeal apotomes of pupae (of known sex) were compared with those of larvae. Since head width is easier to measure on larvae than frontoclypeal dimensions, mathematical relationships between frontoclypeal dimensions and head widths were calculated.

Results and Discussion

Size frequency histograms of head width of fourth and fifth (ultimate) instar larvae and prepupae are shown in figure 18. The pronounced bimodality in fifth instar larvae could imply the presence of a sixth instar, as assumed by Brickenstein (1955). However, head widths of prepupae (as defined by Wiggins 1977) showed the same range as this plot, verifying that these were all ultimate instar larvae (Figure 18). The size frequency of fourth instar larvae also shows a slight bimodality.

To determine that this bimodality of head widths was a sexual dimorphism, the frontoclypeal apotomes of pupae of

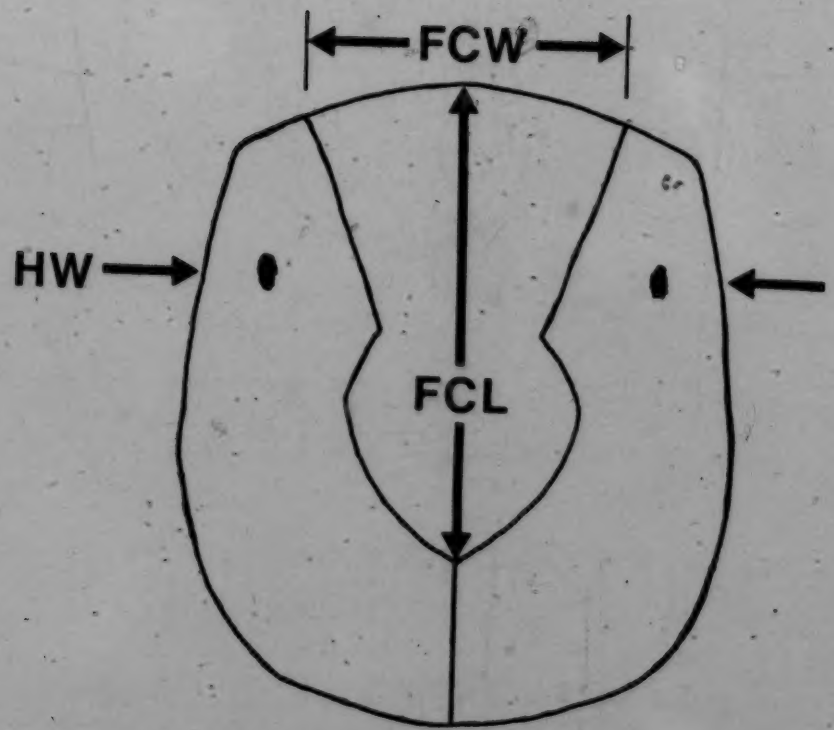

Figure 17. Head of *N. bimaculata* larva showing the dimensions measured. HW=head width, FCL=frontoclypeal apotome length, FCW=frontoclypeal apotome width.

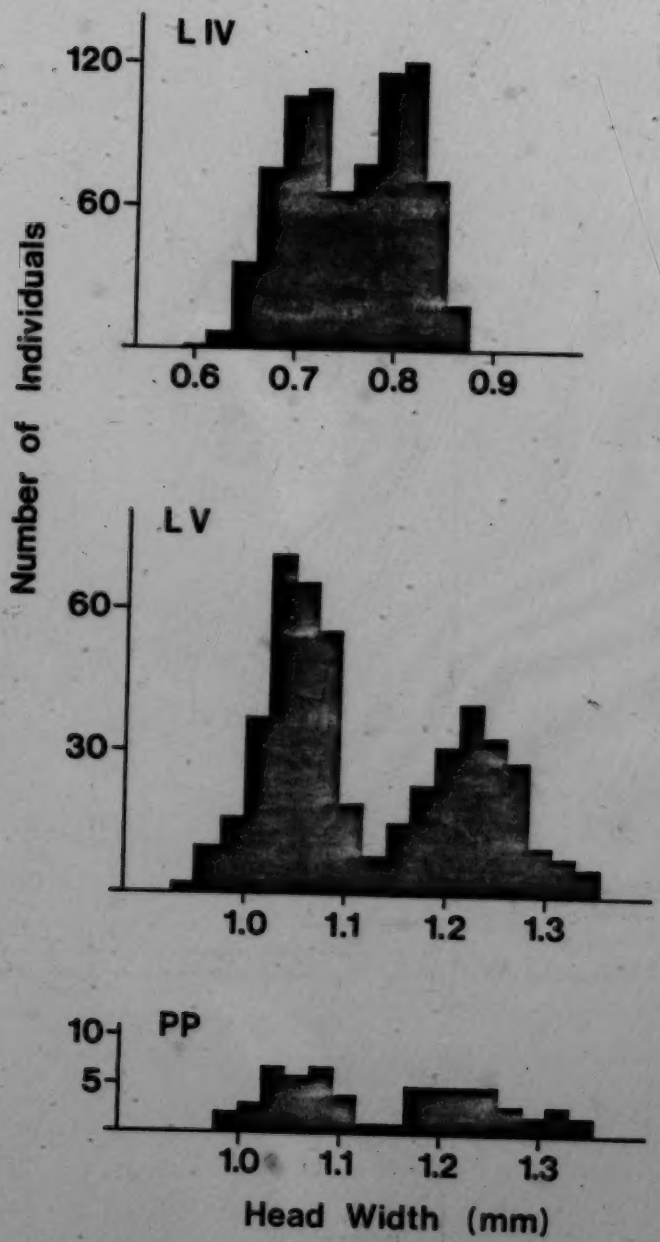

Figure 18. Head width frequency histograms of fourth and fifth instar larvae and prepupae of *N. bimaculata*.

known sex were plotted. The sizes of these sclerites fall into two groups, corresponding to the two sexes (Figure 19).

To relate this size difference to larvae, regressions between larval head width and larval frontoclypeal apotome size were calculated. These relationships are shown in figure 20. This shows that larval head width is strongly correlated with frontoclypeal apotome (FCA) dimensions. Since the FCA sizes are separate for each sex, the bimodal frequency distribution of fifth instar larval head widths must likewise be sex-related. The head width measurements of fifth instar larvae reared to pupation were consistent with these conclusions.

Head width and general body size were the only distinguishable differences between the sexes of larval *N. bimaculata*. Elliott (1982) found that differences in case size and overall size of fifth instar *Odontocerum albicorne* (Scopoli) larvae was sex-related. The magnitude of the size difference between male and female fifth instar larvae of *O. albicorne* is similar to what I found for *N. bimaculata*. In *N. bimaculata* larvae the overlap between the sexes was small in the fifth instar. Assuming that the eight fifth-instar larvae with a head width of 1.128 mm (Figure 18) consist of four males and four females, then they accounted for only 1.5 and 2.3% of males and females respectively. One could disregard individuals that fell within the small region of overlap and use the remainder to test for other sex-related differences (e.g. ecology,

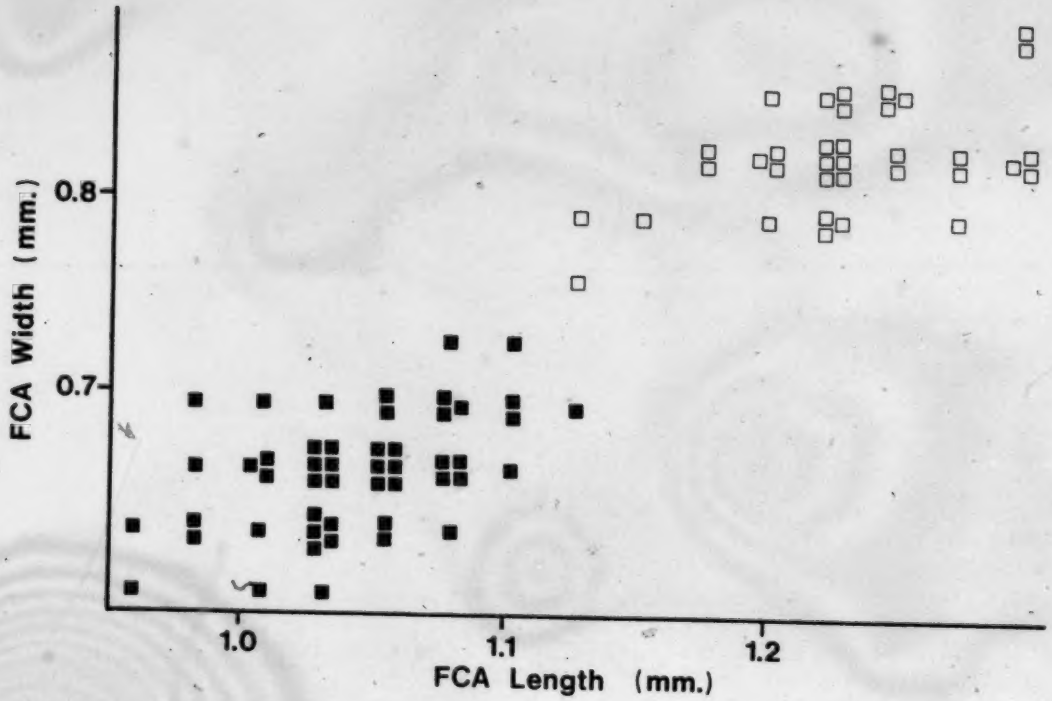

Figure 19. Plot of frontoclypeal apotome size from pupae of *Neureclipsis bimaculata*: males are closed squares, females are open squares.

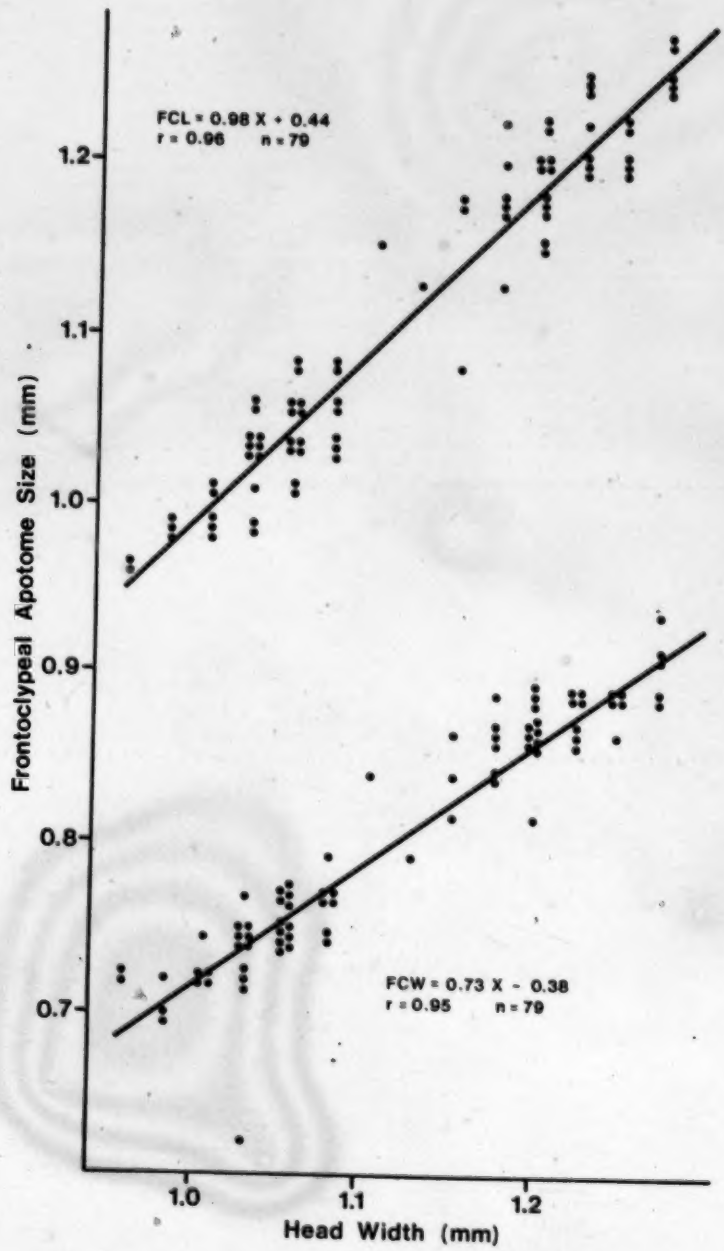

Figure 20. Plot of the relationships between head width and frontoclypeal apotome dimensions in a series of fifth instar larvae.

behaviour, etc.).

The large range of larval sizes within the fifth instar of this species (and other species as well) has no doubt contributed to difficulties interpreting the life cycle. Also, female ultimate instar larvae appear later than the male ultimate instar larvae; this also could lead to the interpretation of an additional larval instar. Some authors have described *N. bimaculata* as being semivoltine based on the wide range of larval sizes present during most of the year (Wesenberg-Lund 1911, Alm 1926). Although *N. bimaculata* may be semivoltine in the localities studied by these authors, the large size variation within single instars should be considered in interpreting life cycle data.

The ability to differentiate the sex of ultimate instar larvae (and to some extent L-IV larvae) permits the analysis of sex-related differences, e.g. differences in the growth rate, and mortality of males and females (see previous chapters).

THESIS DISCUSSION

What determines the distribution of *Neureclipsis bimaculata* populations ?

Of the hypotheses proposed in the Thesis Introduction, some can be rejected or assigned little importance. There is no evidence to suggest that *N. bimaculata* is competitively excluded from other parts of the Sturgeon River. Other filter feeding invertebrates, e.g. *Simulium vittatum* Zetterstedt and species of hydropsychid caddisflies, are common along the entire course of the river, although they are more abundant at the lake outflow. There is no reason *a priori* to suspect that predators could be responsible for the distribution pattern shown by this population of *N. bimaculata*.

Differences in temperature between lake outflows and downstream reaches are unlikely to be important in determining distribution. I found no differences in temperatures at different sites on the Sturgeon River. Since Lac Ste. Anne is shallow, and holomictic (i.e. constantly mixed), the lake experiences approximately the same daily fluctuations in water temperature as do the downstream sites. Carlsson *et al.* (1977) found that the temperatures of a Swedish lake outlet were intermediate to two downstream sites. Although winter temperatures are usually warmer at lake outlets, this difference is unlikely to be of much consequence since *N. bimaculata* do not spin

nets and do not appear to grow in winter in my study area. Also, the water temperature of Lac Ste. Anne is as low as 0.5°C in most winters.

Geomorphology of the lake outlet will be important in determining current velocity and turbulence. However, even though lake outlet reaches tend to be wide and shallow (Carlsson *et al*. 1977), these are not the only wide and shallow locations on the river. In larger rivers, *N. bimaculata* occur irrespective of lake outlets (Popowa 1927, Lepneva 1964, Tachet and Bournaud 1981). This suggests that geomorphology of lake outlets is not a characteristic that would explain the limited distribution *N. bimaculata* larvae in smaller order streams.

Large, sudden fluctuations in discharge and current velocity, e.g. following storms, should be ameliorated by lakes. Although reduced amplitude of fluctuations will mean longer duration, an animal that feeds using a filtering structure, such as the net of *N. bimaculata*, should be better able to adjust to slow changes in discharge.

Silt load (inorganic particulates) will be a determinant of seston quality. Parker and Voshell (1982) suggested that the ratio of organic to inorganic seston in a sample may be an estimate of seston quality. How increases in inorganic particulates, with increasing distance downstream of a lake, affects seston quality and thus larval growth will have to be experimentally determined. Large rivers tend to be silt-laden (Hynes 1970) and *N. bimaculata*

populations manage to live in some of these. This suggests that silt should not be a major influence on distribution.

Current velocity will have important effects on the distribution of *N. bimaculata*. *Neureclipsis bimaculata* larvae are unable to build or maintain nets in swift currents (Brickenstein 1955). Also, turbulence increases as velocity increases and will also affect net building (Smith 1975). Henri Tachet (personal communication) is of the opinion that current velocity is the single most important factor determining distribution of *N. bimaculata* larvae. He found larvae in the Rhône River only where current speed slowed to less than 40 $cm \cdot s^{-1}$.

There are major differences in the prey types available at lake outlets compared to downstream reaches. Although many species of aquatic insects and other invertebrates will drift in any reach of the stream, few of these species can be easily caught in the nets of *N. bimaculata* larvae. Thus prey catchability and abundance will be important in determining distribution. An abundant supply of drifting, limnetic zooplankton at lake outlets and the high efficiency with which the nets capture these animals means that lakes provide the best source of prey. Animal material in the seston will be more nutritious and calorically beneficial to *N. bimaculata* larvae than the highly refractory detritus which is a main component of seston in downstream reaches. With increasing size of rivers there is a trend towards autotrophy, so that seston quality increases in moderately

large rivers (Vannote *et al*. 1980). This is probably why *N. bimaculata* populations are also found in large rivers such as the Rhône and Volga.

Conclusions and Future Research

Given the importance of seston quality to growth of *N. bimaculata* larvae, it would be interesting to test the effects of lake productivity on life history characteristics of filter feeders. The prediction that life cycles should be speeded up downstream of increasingly productive lakes has some support (Tachet 1967, Carlsson *et al*. 1977, Mackay 1979, Parker and Voshell 1982). Population densities should also be proportional to productivity up to a point. Adult weight, and by inference fecundity, may also increase with increasing productivity. Wallace *et al*. (unpublished manuscript) have evidence that *N. bimaculata* individuals grow to larger weights below a productive lake than below two oligotrophic lakes.

In summary, seston quality and current velocities within certain limits seem to be the primary determinants of the distribution of *N. bimaculata* populations. While other ecological constraints may also influence distribution and abundance, seston and current appear to be the most important.

Literature Cited

Alm, G. 1926. Beiträge zur Kenntnis der netzspinnenden Trichopteren-larven in Schweden. Int. Rev. ges. Hydrobiol. 14:233-275.

Alstad, D.N. 1982. Current speed and filtration rate link caddisfly phylogeny and distributional patterns on a stream gradient. Science 216:533-534.

Armitage, P.D. 1976. A quantitative study of the invertebrate fauna of the River Tees below Cow Green Reservoir. Freshwater Biol. 6:229-240.

Armitage, P.D. and M.H. Capper. 1976. The numbers, biomass and transport downstream of microcrustaceans and *Hydra* from Cow Green Reservoir (Upper Teesdale). Freshwater Biol. 6:425-423.

Benke, A.C. and J.B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology 61:108-118.

Brickenstein, C. 1955. Über den Netzbau der Larve von *Neureclpsis bimaculata* L. (Trichopt., Polycentropidae). Abh. Bayer. Akad. Wiss., n.s. 69:1-44.

Brindle, A. 1960. The larva of *Neureclipsis bimaculata* (L.) (Trichoptera, Polycentropidae). Ent. Record 72:244-245.

Carlsson, M., L.M. Nilsson, B. Svensson, S. Ulfstrand and R.S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos 29:229-238.

Chandler, D.C. 1937. Fate of typical lake plankton in streams. Ecol. Monogr. 7:445-479.

Chapman, R.F. 1969. The Insects: Structure and Function.

American Elsevier, New York. 819pp.

Cudney, M.D. and J.B. Wallace. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. Holarctic Ecol. 3:169-182.

Cushing, C.E. Jr. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. Trans. Am. Fish. Soc. 92:216-219.

Edington, J.M. and A.G. Hildrew. 1981. Caseless Caddis Larvae of the British Isles. Freshwater Biol. Assoc. Sci. Publ. 43. 92pp.

Elliott, J.M. 1968. The life history and drifting of Trichoptera in a Dartmoor stream. J. Anim. Ecol. 37:615-625.

Elliott, J.M. 1982. A quantitative study of the life cycle of the case-building caddis *Odontocerum albicorne* (Trichoptera: Odontoceridae) in a Lake District stream. Freshwater Biol. 12:241-255.

Fuller, R.L. and R.J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. 58:2239-2251.

Fuller, R.L. and R.J. Mackay. 1981. Effects of food quality on the growth of three *Hydropsyche* species (Trichoptera: Hydropsychidae). Can. J. Zool. 59:1133-1140.

Georgian, T.J., Jr. and J.B. Wallace. 1981. A model of seston-capture by net-spinning caddisflies. Oikos 36:147-157.

Gotceitas, V. and H.F. Clifford. The life history of *Dicosmoecus atripes* (Hagen) (Limnephilidae: Trichoptera) in a Rocky Mountain stream of Alberta, Canada. Can. J. Zool. (in press).

Gurtz, M.E., J.R. Webster and J.B. Wallace. 1980. Seston dynamics in southern Appalachian streams: effects of

clear-cutting. Can. J. Fish. Aquat. Sci. 37:624-631.

Hickin, N.E. 1967. Caddis Larvae: Larvae of the British Trichoptera. Fairleigh Dickinson Univ. Press. 480pp.

Hildrew, A.G. and C.R. Townsend. 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). Anim. Behav. 28:553-560.

Horridge, G.A. and P.S. Boulton. 1967. Prey detection by Chaetognatha via a vibration sense. Proc. Roy. Soc. B 168:413-419.

Hynes, H.B.N. 1970. The Ecology of Running Waters. Univ. Toronto Press. 555pp.

Hutchinson, G.E. 1967. A Treatise on Limnology. Volume II. Introduction to lake biology and the limnoplankton. Wiley. 1115pp.

Illies, J. 1956. Seeausfluß-Biozönosen lappländischer Waldbäche. Entomol. Tidskr. 77:138-153.

Jansson, A. and T. Vuoristo. 1979. Significance of stridulation in larval Hydropsychidae (Trichoptera). Behaviour 71:167-186.

Lepneva, S.G. 1964. Fauna of the U.S.S.R. Trichoptera Vol. II, No. 1. Israel Program for Scientific Translations.

Maciolek, J.A. and M.G. Tunzi. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream system. Ecology 49:60-75.

Mackay, R.J. 1979. Life history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. 57:963-975.

Mackay, R.J. and G.B. Wiggins. 1979. Ecological diversity in Trichoptera. Ann. Rev. Entomol. 24:185-208.

Merritt, R.W., K.W. Cummins and V.H. Resh. 1978. Collecting, sampling and rearing methods for aquatic insects. In: Merritt, R.W. and K.W. Cummins (eds.). An Introduction to the Aquatic Insects of North America. Kendall/Hunt. Dubuque, Iowa.

Moretti, G.P. and C.C. Sorcetti. 1981. Gregarines in Trichoptera larvae. Proc. 3rd Int. Symp. Trichoptera. 213-217.

Müller, K. 1954. Faunistisch-ökologische untersuchungen in Nordschwedischen Waldbächen. Oikos 5:77-94.

Müller, K. 1982. The colonization cycle of freshwater insects. Oecologia 52:202-207.

Naiman, R.J. and J.R. Sedell. 1979. Benthic organic matter as a function of stream order in Oregon. Arch. Hydrobiol. 87:404-422.

Nimmo, A.P. The Polycentropodidae of Canada, Alaska, and adjacent United States (Trichoptera: Polycentropodidae). The Insects and Arachnids of Canada. Agriculture Canada. (In press).

Oswood, M.W. 1979. Abundance patterns of filter-feeding caddisflies (Trichoptera: Hydropsychidae) and seston in a Montana (U.S.A.) lake outlet. Hydrobiologia 63:177-183.

Parker, C.R. and J.R. Voshell,Jr. 1982. Life histories of some filter-feeding Trichoptera in Virginia. Can. J. Zool. 60:1732-1742.

Pennak, R.W. 1978. Freshwater Invertebrates of the United States. 2nd ed. Wiley-Interscience. 803pp.

Philipson, G.N. 1953. The larva and pupa of *Hydropsyche instabilis* Curtis (Trichoptera, Hydropsychidae). Proc. R. Ent. Soc. Lond. (A) 28:17-23.

Popowa, A.N. 1927. Über die Ernährung der Trichopterenlarven (*Neureclipsis bimaculata* L. und *Hydropsyche ornatula* McLach.). Zeitschrift für

Wiss. Ins.-Biologie. 22:147-159.

Reif, C.B. 1939. The effect of stream conditions on lake plankton. Trans. Am. Microsc. Soc. 58:398-403.

Resh, V.H. 1976. Life histories of coexisting species of *Ceraclea* caddisflies (Trichoptera: Leptoceridae): the operation of independent functional units in a stream ecosystem. Can. Ent. 108:1303-1318.

Robertson, M.R. 1967. Certain limnological characteristics of the La Biche and Wandering Rivers. M.Sc. thesis, University of Alberta.

Sedell, J.R., R.J. Naiman, K.W. Cummins, G.W. Minshall and R.L. Vannote. 1978. Transport of particulate organic material in streams as a function of physical processes. Verh. Internat.Verein.Limnol. 20:1366-1375.

Sheldon, A.L. and M.W. Oswood. 1977. Blackfly (Diptera:Simuliidae) abundance in a lake outlet: test of a predictive model. Hydrobiologia 56:113-120.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W.H. Freeman. 859pp.

Smith, I.R. 1975. Turbulence in lakes and rivers. Freshwat. Biol. Assoc. Sci. Publ. 29: 79pp.

Statzner, B. 1978. The effects of flight behaviour on the larval abundance of Trichoptera in the Schierenseebrooks (North Germany). Proc. 2nd Int. Symp. Trichoptera. 121-134.

Statzner, B. 1979. Der obere und untere Schierenseebach (Schleswig-Holstein). Strukturen und funktionen in zwei Norddeutschen see-ausfluss-systemen, unter besonderer berücksichtigung der makroinvertebraten. PhD Dissertation. University of Kiel.

Tachet, H. 1967. Quelques aspects du cycle biologique de *Plectrocnemia conspersa* (Curtis, 1834) [Trichoptera, Polycentropodidae]. Ann. Limnol. 3:177-184.

Tachet, H. 1971. Aspects descriptifs du comportement alimentaire chez la larve de *Plectrocnemia conspersa* (Trichoptera, Polycentropodidae). Z. Tierpsychol. 28:175-184.

Tachet, H. 1977. Vibrations and predatory behaviour of *Plectrocnemia* larvae. Z. Tierpsychol. 45:61-74.

Tachet, H. and M. Bournaud. 1981. Cycles biologiques des Hydropsychidae et d'un Polycentropodidae (Trichoptera) dans le Rhône en amont de Lyon. Proc. 3rd Int. Symp. Trichoptera. 347-364.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Wallace, J.B., R.C. Petersen and L. Petersen. Factors affecting the net construction of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae). Unpublished manuscript.

Ward, G.M. and K.W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ecology 60:57-64.

Waters, T.F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10:91-164.

Waters, T.F. 1979. Benthic life histories: summary and future needs. J. Fish. Res. Board Can. 36:342-345.

Wesenberg-Lund, C. 1911. Biologische studien über netzspinnende, campodeoide Trichopterenlarven. Int. Revue ges. Hydrobiol. Hydrogr. Suppl. 3:1-64.

Wesenberg-Lund, C. 1943. Biologie der Süsswasserinsekten. Springer, Berlin.

Wiggins, G.B. 1977. Larvae of the North American Caddisfly Genera (Trichoptera). Univ. Toronto Press. 401pp.

Wiggins, G.B. and J.S. Richardson. 1982. Revision and synopsis of the caddisfly genus *Dicosmoecus* (Trichoptera: Limnephilidae; Dicosmoecinae). Aquatic Insects (in press).

Appendix 1: Total numbers of *N. bimaculata* larvae, prepupae, and pupae per sample. Only completely sorted samples included. Samples with no individuals not listed.

Date	N	Sampler	Number of individuals per sample
6 Nov 80	5	Lee	16 14 7 5 1
	7	Core	23 10 6 5 1
18 Nov 80	54	Core	7 3 3 2 1 1 1 1
18 Jan 81	30	Core	12 12 6 6 1 1
17 Mar 81	27	Core	20 10 4 2 1 1 1 1 1 1
18 Apr 81	27	Core	10 4 2 1 1 1 1 1 1 1 1 1 1
5 May 81	5	Lee	90 69 41 19 19
19 May 81	8	Lee	204 104 50 45 31 26 17 3
2 Jun 81	7	Lee	36 27 23 18 3 1 1
15 Jun 81	8	Lee	29 19 15 11 10 8 4 4
29 Jun 81	5	Lee	141 88 43 5 2
13 Jul 81	6	Lee	987 601 525 110 75 52
3 Aug 81	9	Lee	1171 426 60 23 13 13 10 2 2
17 Aug 81	5	Lee	168 132 86 4 2
31 Aug 81	6	Lee	151 94 19 11 4
14 Sep 81	6	Lee	224 32 31 24 10 1
15 Oct 81	8	Lee	69 25 17 10 7 1 1 1
7 Dec 81	11	Lee	67 28 20 15 5 4 4 2 1 1 1
7 Jun 82	14	Ekman	8 8 7 6 5 5 3 2 2 2 2

Appendix 2: Numbers of samples of fourth and fifth instar larvae used for population estimates. Only samples collected in the Lee sampler included.

Date	Number of Samples
6 Nov 80	5
5 May 81	5
19 May 81	9
2 Jun 81	7
15 Jun 81	20
29 Jun 81	10
13 Jul 81	6
3 Aug 81	21
17 Aug 81	8
31 Aug 81	7
14 Sep 81	6
15 Oct 81	7
7 Dec 81	11

Appendix 3: Response times of *N. bimaculata* larvae to different prey items in the net (seconds). Only includes prey items to which larvae responded.

Live *Daphnia*	Dead *Daphnia*	chironomid
260	290	840
96	272	665
50	246	345
47	211	256
31	183	192
25	154	137
14	105	66
11	83	65
10	72	30
10	45	18
9	20	3
9	16	
8	11	
6	10	
6	5	
5		
3		
3		
3		
3		
3		
3		
3		

Appendix 4: Preliminary list of the invertebrate taxa found in the Sturgeon River at Lac Ste. Anne, Alberta.

Cnidaria		
		Hydra sp.
Turbellaria		
Hirudinea		
Amphipoda		
		Hyallela azteca
Ephemeroptera		
	Leptophlebiidae	*Leptophlebia cupida*
	Baetidae	*Baetis tricaudatus*
		Baetis brunnicolor
		Callibaetis
	Caenidae	*Caenis*
Odonata		
	Aeshnidae	*Aeshna* sp.
Trichoptera		
	Hydroptilidae	*Hydroptila waubesiana*
		Hydroptila sp.
		Orthotrichia sp.
	Hydropsychidae	*Hydropsyche* bifida group
		Cheumatopsyche sp.
	Polycentro-podidae	*Neureclipsis bimaculata*
		Polycentropus remotus
	Limnephilidae	*Anabolia bimaculata*
		Glyphopsyche irrorata
		Limnephilus externus
		Limnephilus infernalis
		Limnephilus nigriceps
		Nemotaulius hostilis
	Phryganeidae	*Agrypnia straminia*
		Agrypnia sp.
		Phryganea cinerea
	Brachy-centridae	*Brachycentrus lateralis?*
	Helico-psychidae	*Helicopsyche borealis*
	Leptoceridae	*Triaenodes (Ylodes) frontalis*
		Triaenodes injusta?
		Ceraclea transversa
		Ceraclea tarsipunctata
		Ceraclea excisa
		Oecetis immobilis
		Oecetis inconspicua
		Mystacides interjecta
		Mystacides sepulchralis

Appendix 4: continued-

Coleoptera		
	Chrysomelidae	*Haemonia nigricornis*
	Dytiscidae	*Laccophilus biguttatus*
		Hydroporus superioris
		Deronectes elegans
		Ilybius sp.
		Colymbetes sculptilis
	Haliplidae	*Haliplus* sp.
	Gyrinidae	
Gastropoda		
		Ferrisia
	Lymnaeidae	*Lymnaea*
	Valvatidae	*Valvata tricarinata*
Pelecypoda		
	Pisidiidae	
	Anodontidae	

Note: Identifications were provided by D.C. Currie (simuliid), R. Roughley (Coleoptera), and D.A. Soluk (Ephemeroptera). Dr. C. Parker verified my Trichoptera identifications.